POPULATION DYNAMICS OF NORTHERN BOBWHITES IN SOUTHERN TEXAS

A Dissertation

by

STEPHEN J. DEMASO

Submitted to the Office of Graduate Studies of
Texas A&M University and Texas A&M University–Kingsville
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2008

Major Subject: Wildlife Science

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Approved by:

Co-Chairs of Committee,	Fidel Hernández
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ABSTRACT

Population Dynamics of Northern Bobwhites in Southern Texas. (December 2008)

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Northern bobwhites (*Colinus virginianus*) are an important cultural, ecological, and economical part of the southern Texas landscape. I used radio-telemetry data from 2000–2005, part of a long-term, bobwhite study in southern Texas, to test the nest-concealment hypothesis, develop a stochastic simulation model for bobwhite populations, and evaluate the influence of brush canopy coverage (BCC) on short- and long-term demographic performance of bobwhites.

Bobwhite nests tend to be situated in taller and denser vegetation than would be expected if nest-site location was a random process. I compared 4 microhabitat variables between successful (n = 135) and depredated nests (n = 118). I documented similar microhabitat attributes between successful and depredated nests. The discriminant function correctly classified only 48–59% of nest fates into the correct group, but only 18% of the variation in nest fate. Thus, my results did not support the nest-concealment hypothesis.

My stochastic simulation model for bobwhite populations is based on difference equations (Δt = 3 months) and simulations run for 100 years using STELLA® 9.0.2. The

probability of persistence for 100 years for the spring population was 74.2% and 72.5% for the fall population. Simulated population parameters were similar to those observed in the field for 5 of 6 population parameters. Only simulated male adult annual survival differed by 275.0% from field estimates. Despite this difference, my model appears to be a good predictor of bobwhite populations in the Rio Grande Plains of Texas.

I estimated bobwhite density, survival, and production (proportion of hens nesting, nesting attempts per hen, and clutch size) in 3 study areas with ~10%, ~25%, and >30% BBC. All demographic parameters were similar among the 3 BCC classes. However, simulation modeling indicated that long-term demographic performance was greater on the ~25% and >30% BCC classes. The probability of fall population persistence was greater in the ~25% (90.8%) and >30% (100.0%) BCC classes than in the ~10% BCC class (54.2%). My study highlights the shortcoming of considering only short-term effects when comparing habitat given that short- and long-term effects of habitat on demographic performance can differ.

DEDICATION

To Tara, Tori, Ella, and Angie, thank you for all the great bird hunts and days in the field together. I apologize for all the nights and weekends you had to endure next to the couch or on a cold, university office floor instead of hunting. You are the best bird dogs a game bird biologist could be blessed with. Piper Ann you are the lucky one!

To my brother Michael J. DeMaso, you are the best! Thank you for always being there!

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Finally, thanks to all my friends with the Oklahoma Department of Wildlife Conservation, Texas Parks and Wildlife Department, Southeast Quail Study Group, and

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TABLE OF CONTENTS

CHAPTER Page

LIST OF FIGURES

FIGURE Page

LIST OF TABLES

TABLE Page

CHAPTER I

INTRODUCTION

Northern bobwhites (*Colinus virginianus*) have been declining since about 1880, with declines occurring over 75% of the species range in the United States (Leopold 1931:26, Errington and Hammerstrom 1936:382, Lehmann 1937:8, Guthery 2002:3). These initial declines prompted research on the ecology and life history of bobwhites (Stoddard 1931). Since then, much research has been devoted to the species (Rosene 1969, Lehmann 1984, Roseberry and Klimstra 1984, Hernandez et al. 2002a). However, despite this wealth of information, bobwhite populations continue to decline.

The decline of bobwhite populations has been attributed to a variety of factors including predators, fire ants, and pesticides. Although these factors may play a role at a local scale, the primary cause of the decline has been the cumulative effect of large-scale deterioration of bobwhite habitat with advancing plant succession (Roseberry et al. 1979, Fies et al. 1992), intensive monoculture farming (Vance 1976, Exum et al. 1982, Roseberry 1993), and intensive timber management (Brennan 1991). These declines have increased because bobwhite management has been based on several dogmatic principles for decades. In recent years, however, new tools available to researchers (i.e., modeling, geographic information systems [GIS], etc.) have shown that many of the previously held beliefs in bobwhite biology and management are incomplete or false

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This dissertation follows the style of the Journal of Wildlife Management.

(Guthery 2002:3).

Texas is one of the last strongholds for bobwhites in North America (Rollins 2002). However, recent analyses of Texas Parks and Wildlife Department bobwhite-survey data has shown that Texas is not immune from the declines that have occurred throughout the rest of the species range (DeMaso et al. 2002). These more recent accounts of the bobwhite decline have relied on either the Christmas Bird Count (Brennan 1991) or the North American Breeding Bird Survey (Church et al. 1993, Brady et al. 1998) which allow for more quantitatively rigorous analyses than the earlier, descriptive accounts. Using GIS, Peterson et al. (2002) documented that bobwhite abundance declined from 1978 to 1997 in the Rio Grande Plains and Rolling Plains ecoregions (Gould 1975) despite relatively extensive rangeland cover (i.e., >50% of the landscape).

The apparent bobwhite decline in Texas is difficult to interpret because even in areas saturated with usable space (Guthery 1997), bobwhite populations still can exhibit considerable annual variability due the influence of weather on bobwhite populations (Lehmann 1953, Kiel 1976, Guthery et al. 1988, Bridges et al. 2001, Lusk et al. 2002). Weather can account for about 30% of the variability observed for bobwhite populations in semiarid environments (Rice et al. 1993). In southern Texas, there appears to be an alternation of 20–30-year wet and dry cycles, with a potential transition into a dry period that started in the late 1970s (Norwine and Bingham 1985). Therefore it is difficult to decipher whether the bobwhite decline in southern Texas is real, or simply an artifact of naturally-occurring dry periods.

Bobwhite populations are complex, dynamic systems consisting of and affected by numerous biotic and abiotic variables (Roseberry and Klimstra 1984). In order to better understand the dynamics of bobwhite populations in Texas, a quantitative population model is warranted. My research used data from the South Texas Quail Research Project to develop a population model for bobwhites in southern Texas. The South Texas Quail Research Project is an intensive, long-term northern bobwhite radio-telemetry project that has been conducted in Brooks County, Texas since 1998. My dissertation consists of 3 chapters, namely: (1) Does Bobwhite Nesting Habitat Influence Nest Success?, (2) A Radio-telemetry based simulation model for Northern Bobwhites in Southern Texas, and (3) Habitat Influence on Demographic Performance: Effect of Brush Cover on Northern Bobwhite Abundance, Productivity, and Survival in Southern Texas.

CHAPTER II

DOES BOBWHITE NESTING HABITAT INFLUENCE NEST SUCCESS?

Nest-site location in northern bobwhite is a nonrandom process. Research in Kansas (Taylor et al. 1999) western Oklahoma (Townsend et al. 2001) and Texas (Hernández et al. 2003, Lusk et al. 2006, Arredondo et al. 2007, Rader et al. 2007) indicates bobwhites select nest sites that differ from random points in the surrounding area. Given that bobwhite nest-site selection occurs nonrandomly, it is logical to suspect that a reason exists for the selection of particular nest sites. The most common hypothesis used to explain nonrandom nest-site selection is that better nest concealment (i.e., selecting an inconspicuous nest site) reduces depredation risk (Martin and Roper 1988).

Evidence for the nest-concealment hypothesis has been ambiguous. Research on many avian species has provided evidence both for (Nice 1937, Nolan 1978, Martin and Roper 1988, Martin 1992, Norment 1993, Gregg et al. 1994) and against (Roseberry and Klimstra 1970, Gottfried and Thompson 1978, Best and Stauffer 1980, Holoway 1991, Colwell 1992, Shieck and Hannon 1993, Filliater et al. 1994, Howlett and Stuchbury 1996, Wilson and Cooper 1998, Braden 1999) the hypothesis. The reasons for this ambiguous evidence are not clear, but could extend from the fact that past research testing this hypothesis spanned across a large geographic area and used a broad suite of avian species with diverse life histories. Focusing on a single species or guild therefore could provide a more insightful assessment of the hypothesis. In bobwhites, annual productivity may be the most important factor associated with changes in annual

population size (Roseberry and Klimstra 1984:133), therefore it is intuitive to expect strong selection pressure on factors that maximize productivity. Because nest depredation has been identified as a potential limiting factor for bobwhite populations, one could hypothesize that selection pressure favored nest sites with habitat attribute minimizing the probability of nest depredation.

Wildlife biologists often provide species-specific habitat management recommendations based on habitat–use knowledge (Arredondo et al. 2007, Rader et al. 2007). If microhabitat differed between successful and depredated nest sites, then management recommendations could be refined to create vegetation characteristics that favored successful nests. My objectives were to: (1) compare microhabitat variables between successful and depredated nests using univariate analysis, (2) describe the relationship among microhabitat variables and nest fate in multivariate space using discriminant function analysis, and (3) determine the extent to which microhabitat variables measured at bobwhite nest sites were correlated.

STUDY AREA

The study area is located on a private hunting lease on the Encino Division of King Ranch, Brooks County, Texas which lies within the Rio Grande Plains ecoregion (Gould 1975). The study area consisted of 3 spatially-independent experimental units (i.e., pastures): North Viboras (1,966 ha), La Loba (1,379 ha), and Cuates (1,240 ha). Experimental units were arranged north to south, respectively, and were separated by ~5 km from each other. A woody cover gradient occurred from north to south, with woody

cover decreasing on a southerly gradient. Woody canopy cover was >30% (North Viboras), ~25% (La Loba), and ~10% (Cuates) (Rusk 2006).

Vegetation in the Rio Grande Plains ecoregion is characterized as a mixed-brush community (Scifres 1980:30). Vegetation specific to the study area consisted predominantly of honey mesquite (*Prosopis glandulosa*), huisache (*Acacia smallii*), granjeno (*Celtis pallida*), live oak (*Quercus virginiana*), and pricklypear cactus (*Optuntia lindheimeri*) (Hernández et al. 2002). Predominant forbs included croton (*Croton* spp.), sunflower (*Helianthus annuus*), dayflower (*Commelina erecta*), and partridge pea (*Chamaecrista fasciculata*) (Hernández et al. 2002). Common grasses included little bluestem (*Schizachyrium scoparium*), paspalum (*Paspalum* spp.), three awn (*Aristida* spp.), gulf cordgrass (*Spartina spartinae*), King Ranch bluestem (*Bothriochloa ischaemum*), Kleberg bluestem (*Dichanthium annulatum*), sandbur (*Cenchrus incertus*), red lovegrass (*Eragrostis secundiflora*), and buffelgrass (*Pennisetum ciliare*) (Hernández et al. 2002).

Climatic conditions are classified as semi-arid, sub-humid and are characterized by a high rate of evaporation (Williamson 1983). The months of June and September receive the greatest amount of precipitation. Monthly precipitation ranges from 1.4–13.0 cm with a mean annual rainfall of 65.4 cm (Williamson 1983). The 33-year mean temperature is 22.3 C (range 13.1–29.8 C). January is the coldest month ($\bar{x}$ = 13.1 C), and July is the hottest month ($\bar{x}$ = 29.8 C) (Williamson 1983).

METHODS

Telemetry

I captured bobwhites using standard funnel traps (Stoddard 1931:442) and night-netting (Labisky 1968) through the study. Individuals were classified by sex and age (Rosene 1969:44–54), leg-banded, and birds weighing over 150 g were fitted with a 5–6 g neck-loop radio transmitter (Shields et al. 1982) (American Wildlife Enterprises, Tallahassee, Florida, USA). Radio-marked bobwhites were located ≥2 weekly and ≥3/week during the nesting season (Apr–Oct). I used radio-marked bobwhites to locate nests, as judged from consecutive locations of a bird at the same point. When a nest was found, I continued monitoring until the nest was terminated (i.e., abandoned, depredated, or hatched). Once a nest was terminated, I collected demographic and habitat data at the nest site.

Nest fates were classified as successful (the nest hatched ≥1 egg), abandoned (all eggs remained intact, but the incubating adult bird did not complete incubation), depredated (the nest was depredated by a predator, ≥1 egg was destroyed, and the adult bird did not return to complete incubation), other (miscellaneous causes of failure or the fate of the nest could not be identified). Abandoned (n = 22) and other (n = 4) nest fates were deleted from the analysis, which represented 9.3% of the total nest fates (n = 279).

Microhabitat Variables at Nest Sites

At each nest site, I measured 4 microhabitat variables: mean nest-clump diameter, nest-vegetation height, volume of cover, and suitable nest-clump density. I determined mean nest-clump diameter based on 2 measurements for a nest, a north-south

and an east-west measurement. Mean nest–clump diameter was calculated as the average of the 2 measurements. I measured nest-vegetation height by placing a meter stick in the center of the nest and measured the lowest visible reading of the vegetation directly over the nest site. To measure volume of cover (VOC), the nesting substrate was envisioned as a cylinder. I used the nest–clump diameter and nest height to calculate the VOC:

$$VOC = \pi(\text{nest radius})^2(\text{nest height})$$

where nest radius = mean nest–clump diameter/2.

I used VOC to quantify egg concealment within the nesting substrate. Nest-clump density was estimated using the point-center quarter method (Cottam and Curtis 1949, Cottam et al. 1953, Cottam and Curtis 1956). Four quadrants (N, E, S, and W) were delineated at each nest with the nest site being in the center. I measured the distance to the nearest suitable nest clump in each quadrant defined as a bunchgrass at least 25 cm wide × 25 cm high (Lehmann 1984:177). These distances were used to calculate the density as described by Cottam and Curtis (1949).

Statistical Analysis

I used Chi–square tests to test whether nest success was independent of years (Agresti 1996). I used PROC CORR (SAS Institute, Inc., 2006) to test for any correlations among microhabitat variables measured at nest sites. I used 95% confidence intervals for univariate comparisons of microhabitat variables between successful and depredated nests (Johnson 1999). For multivariate comparisons, I used discriminant function analysis to explore and describe the habitat gradients that best discriminated between

successful and depredated bobwhite nests (McGarigal et al. 2000). Backward stepwise selection was used to eliminate unnecessary microhabitat variables ($P \geq 0.05$ for removal) and select the most useful subset of variables (Klecka 1980). I used the jackknife procedure (Efron 1982), cross-validation (SAS Institute, Inc., 2006) and Cohen's Kappa Statistic (Cohen 1960, Titus et al. 1984) as measures of improvement in classification over that expected by random assignment. Tests of whether classification results where statistically different from chance were based on the kappa statistic (Titus et al. 1984). Graphical representation of the canonical scores was used to assess the importance of the discriminant function. A Chi-square test (Morrison 1976) was used to evaluate the equality of the variance–covariance matrices between groups. The correlation between the canonical function and individual variables (total structure coefficients) were used to examine the relative importance of individual microhabitat variables (McGarigal et al. 2000).

RESULTS

I monitored 253 bobwhite nests (n = 135 successful; n = 118 depredated) during 2001–2005 (Fig. 2.1). The number of nests monitored ranged annually from 28 in 2002 to 72 in 2003 (Fig. 2.1). Apparent nest success differed annually ($X^2 = 11.21$, df = 4, P = 0.0243); however, this relationship was driven primarily by data from 2003 ($X^2 = 6.72$, df = 1, $P = 0.0095$) (Fig. 2.1). Apparent nest success was similar across all other years ($P > 0.1317$) (Fig. 2.1).

I documented no difference in microhabitat variables between successful and depredated nests using 95% confidence intervals (Fig. 2.2). Nest-clump diameter, nest-

vegetation height, and VOC were positively correlated ($P < 0.0001$) with each other (Table 2.1). This is the result of nest-clump diameter and nest-vegetation height being

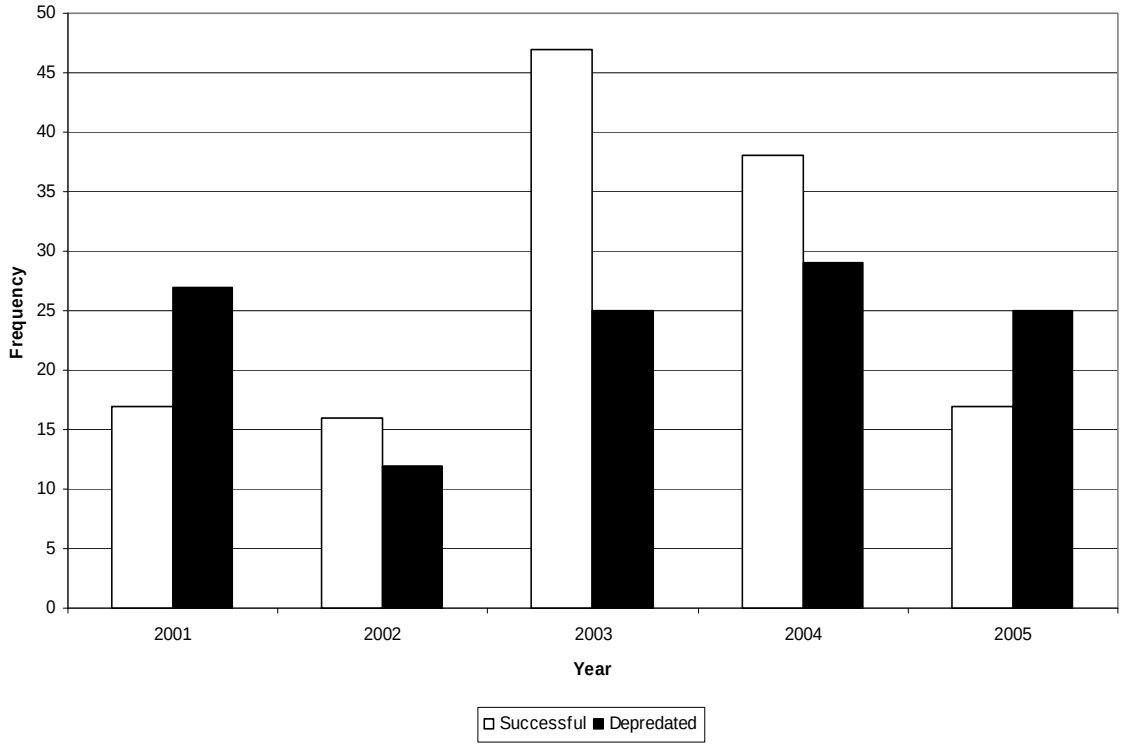

Figure 2.1. Frequency of successful and depredated northern bobwhite nests during May–September, 2001–2005, Brooks County, Texas, USA.

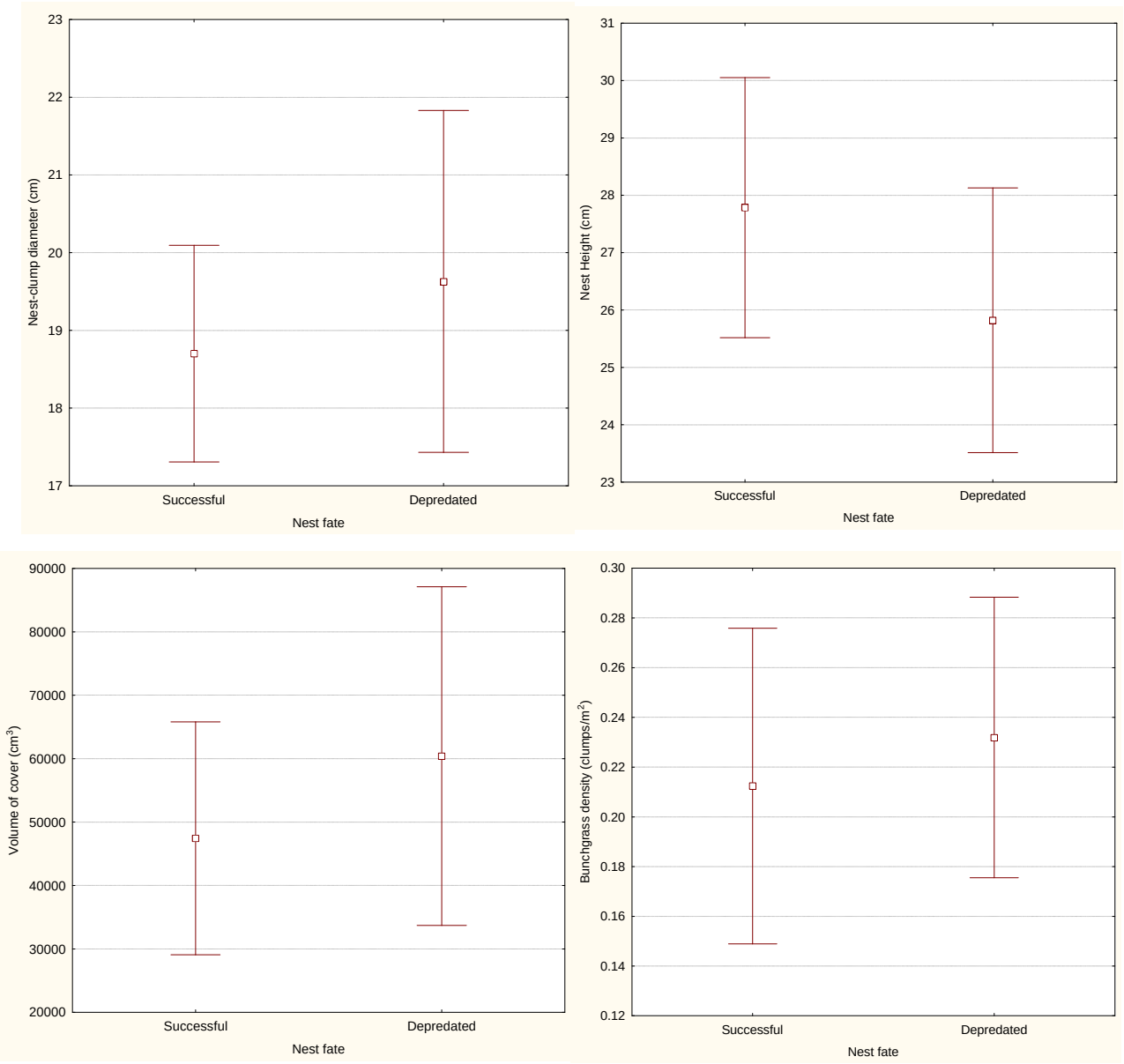

Figure 2.2. Mean and 95 percent confidence intervals for nest-clump diameter, nest-vegetation height, volume of cover, and nest-clump density at successful and depredated northern bobwhite nests during May–September, 2001–2005, Brooks County, Texas, USA.

Table 2.1. Correlation matrix for microhabitat variables measured at successful and depredated northern bobwhite nest-sites (*n* = 253) during May–October, 2001–2005, Brooks County, Texas, USA.

	Microhabitat variable			
Microhabitat variable	Nest–clump diameter	Nest–vegetation height	Volume of cover	Nest–clump density
Nest–clump diameter				
r	1.0000	0.5517	0.7982	0.0623
P–value		<0.0001	<0.0001	0.3238
Nest–vegetation height				
r	0.5517	1.0000	0.7617	0.0225
P–value	<0.0001		<0.0001	0.7215
Volume of cover				
r	0.7982	0.7617	1.0000	-0.0311
P–value	<0.0001	<0.0001		0.6221
Nest–clump density				
r	0.0623	0.0225	-0.0311	1.0000
P–value	0.3238	0.7215	0.6221	

used to calculate VOC, which was used to quantify egg concealment within the nesting substrate.

The 2-group discriminant function analysis of the original 4 microhabitat variables resulted in microhabitat variables (nest-vegetation height and VOC) at bobwhite nest sites showed that a significant function (Eigenvalue = 0.035, Wilk's lambda = 0.97, $P = 0.0139$) successfully classified 48 to 59% of nest fates into the correct group (Table 2.2, Fig. 2.3). Nest fates overlapped considerably (42–52% of the nest fates were misclassified) and the classification results were no better than chance (Kappa statistics, $P > 0.8628$; Table 2.2). Both nest-vegetation height and volume of cover contributed significantly (F-test, $P < 0.0076$) to the discriminant function. The within covariance matrices for successful and depredated nests were unequal ($X^2 = 22.27$, $P < 0.0001$). Nest-vegetation height was the most important variable in the discriminant function (total structure coefficient = 0.4107) followed by VOC (total structure coefficient = -0.2778). The discriminant function explained a low amount of the variation (18%) in nest fate. Based on my multivariate analysis, successful nests were characterized by higher nest–vegetation height and lower VOC (Fig. 2.3).

DISCUSSION

My data do not support the nest-concealment hypothesis. This finding corroborates past research from southern Illinois (Klimstra and Roseberry 1975), southwestern Georgia (Simpson 1976), western Oklahoma (Townsend et al. 2001), and southern Texas (Lehmann 1946, 1984, Rader et al. 2007). These studies documented no difference in microhabitat variables between successful and unsuccessful nests (i.e., depredated and

Table 2.2. Classification results from discriminant analysis of nest fates of northern bobwhite nest microhabitat variables, by classification method, 2001–2005, Brooks County, Texas, USA.

Classification method	Actual nest fate	No. of nests	Predicted nest fate: Successful	Predicted nest fate: Depredated	Overall
Pooled					
	Successful	135	75 (55.6%)	60 (44.4%)	
	Depredated	118	45 (38.1%)	73 (61.9%)	58.5%[a]
Jackknife					
	Successful	135	127 (94.1%)	8 (5.9%)	
	Depredated	118	107 (90.7%)	11 (9.3%)	48.3%[b]
Cross validation					
	Successful	135	126 (93.3%)	9 (6.7%)	
	Depredated	118	107 (90.7%)	11 (9.3%)	48.7%[c]

[a]Correct classification significantly better than chance, Kappa = 0.1728, P = 0.8628.

[b]Correct classification significantly better than chance, Kappa = 0.1198, P = 0.9046.

[c]Correct classification significantly better than chance, Kappa = 0.1202, P = 0.9043.

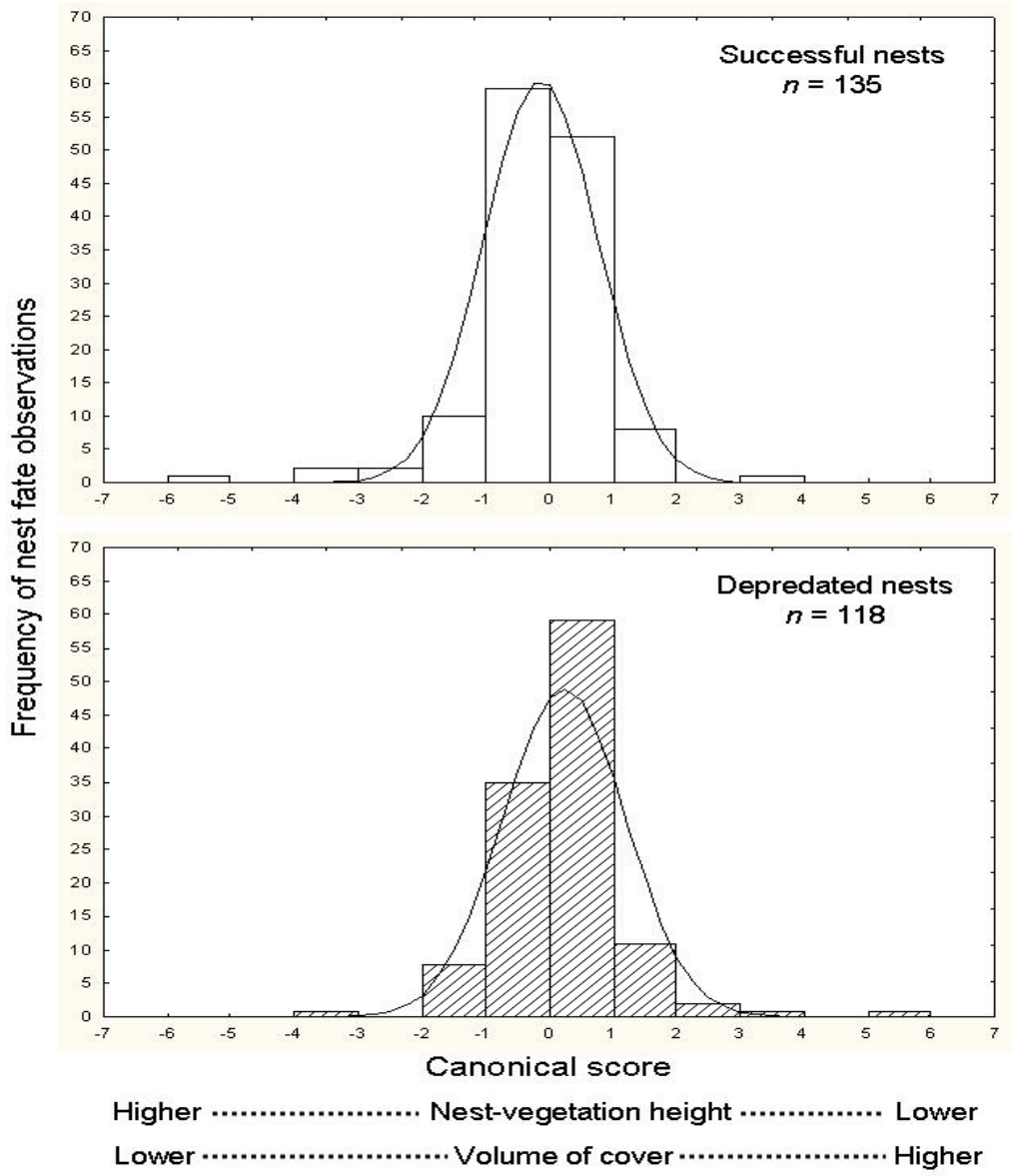

Figure 2.3. Variation in northern bobwhite nest fates during May–September, 2001–2005, Brooks County, Texas, USA, based on a 2-group discriminant analysis. Descriptive statistics of data used in this analysis are presented in Figure 2.2. Statistics for the discriminant analysis are given in Table 2.2.

all other failure causes combined). However, direct comparisons between my study and past research is limited because of differences in nest-fate comparisons (successful vs. depredated and successful vs. unsuccessful, respectively). A true test of the nest-concealment hypothesis involves comparison of microhabitat between successful and depredated nests. Using this approach, research in Kansas (Taylor et al. 1999) did report differences in microhabitat variables between successful and depredated nests. Taylor et al. (1999) reported that patches (blocks or strips of habitat containing 5 random locations where vegetation was measured $\leq$200 m of the respective nest site) containing successful bobwhite nests had less relative shrub cover and taller vegetation than those containing depredated nests.

Because microhabitat variables and methods of collecting data at nest sites varied between my study and Taylor et al. (1999), Lusk et al. (2006), unifying these disparate results is difficult. A common finding among studies is that taller vegetation height at nest sites appears to be a distinguishing characteristic of successful nests (Taylor et al. 1999, Lusk et al. 2006). However, most research does not suggest a definitive relationship between microhabitat and bobwhite nest fate which could indicate that nest fate is influenced largely by chance (i.e., predation as a random process). I propose 8 non-mutually exclusive explanations why at least some prior research has been unable to detect differences in microhabitat variables between successful and depredated (or unsuccessful) bobwhite nests. I deem the first 4 as the most likely explanations, but evaluate the plausibility of all 8 based on evidence from the ornithological literature.

1. *Nest-site vegetation may not determine risk of nest depredation (Braden 1999).*

It is plausible that nest–site vegetation does not influence the probability of nest depredation. Theory suggests that nest placement may be set for a species over a large geographic area based on events during speciation or their evolutionary history (Martin 1993) possibly decoupling the habitat–nest fate relationship. Assuming northern bobwhites cannot influence nest fate through nest placement, how then do they compensate for fitness lost through nesting failure? Filliater et al. (1994) postulated that northern cardinals (*Cardinalis cardinalis*) nest repeatedly within the breeding season because of increased likelihood of success. Cox et al. (2005) reported that bobwhites hens had 1.7 nesting attempts/hen for all hens that entered the nesting season and 3.1 nesting attempts/hen for hens that survived to 15 September in western Oklahoma. Multiple nesting attempts may be one of many adaptive responses species use to compensate for a nest-site selection process that operates independent of predation risk.

2. *Selected microhabitat variables may not be the relevant ones to assess risk of nest depredation (Dion et al. 2000).*

   Microhabitat variables deemed important by scientists may not be ones used by organisms to select nest sites. Birds and predators may perceive differences in vegetation characteristics that may have been undetected by sampling (Dion et al. 2000). Alternatively, small effects may have been present, but were not detectable or measurable. This is because birds have selected nest sites that are a small subset of all nest sites available, vegetation differences among nest sites are small compared to the potential differences among randomly selected nest sites. Once this level of

selection has occurred, it would be very difficult to detect differences in microhabitat variables. Many habitat variables have been measured at bobwhite nest sites (Taylor et al. 1999, Townsend et al 2001, Lusk et al. 2006, Rader et al. 2007); however, few appear to be important concerning nest fate. Because the decision rules used by organisms to select nest sites are unknown, this explanation is impractical to test.

3. *Nest-site selection is governed by factors independent of predation risk (Walsberg 1985).*

   If nest placement is governed by factors unrelated to predation risk, then microhabitat would not be expected to influence nest fate. Recent research indicates that factors such as habitat imprinting to natal sites may be strong drivers of nest-site location (Davis and Stamps 2004). In addition, thermal environment is another factor that could be governing habitat selection (Calder 1973, Bartholomew et al. 1976, Walsberg 1986, Webb and Rogers 1988, and Jenni 1991). Bobwhites in semi–arid environments may be selecting nest sites from a thermal environment perspective rather than risk of predation (Guthery et al. 2005). Guthery et al. (2005) reported that thermal stress (i.e., gular flutter) was a common occurrence for incubating bobwhites in western Oklahoma and that incubating bobwhites appeared to protect nest contents more rigorously from hyperthermia than from hypothermia. Minimizing thermal stress (and not predation risk) therefore may be the primary driver of the nest-site selection process in bobwhites.

4. *Landscape effects may override selection effects of nest placement (Braden 1999).*

Increased depredation of grassland bird nests has been associated with fragmentation and edge effects (Vickery et al. 1992, Burger et al. 1994, Herkert et al. 2003). Thus, landscape effects, through fragmentation processes, may override selection effects on nest placement, accounting for the inability to detect a relationship between microhabitat variables at the nest site and nest fate. Burger et al. (1994) and Herkert et al. (2003) report that grassland-bird nests located in larger patches had lower depredation rates than nest located in smaller patches. Over the past 25 years, my study area has been grazed, prescribed burned, and brush cleared (both by mechanical and herbicide treatments) resulting in possibly altered degrees of landscape heterogeneity. Bowman and Harris (1980) found that spatial heterogeneity of vegetation decreased raccoon foraging efficiency significantly more than nest concealment. Although the effects of landscape heterogeneity cannot readily account for the failure to detect a relationship between microhabitat variables and nest fate, its effect cannot be discounted.

5. *The occurrence of a generalized nest predator community on my study area is different from a specialized predator community that focus on depredating just nests (Zimmerman 1984, and Howlett and Stutchberry 1996).*

   Nest predators on my study area included coyote (*Canis latrans*), striped skunk (*Mephitis mephitis*), American badger (*Taxidea taxus*), raccoon (*Procyon lotor*), bobcat (*Lynx rufus*), native fire ants (S*olenopsis xyloni*), rats, and snakes (Rader et al. 2007). This represents a generalized nest predator community on my study area. Several factors may mask the importance of microhabitat variables and their

contribution to nest concealment. First, nest depredation to some extent is a stochastic event; some nest predators will find nests by chance alone. Second, the chance that a nest is depredated may depend more on its proximity to the home range of a potential nest predator than to subtle concealment factors. Third, if nocturnal predators are important predators of bobwhite nests, and if these predators locate nest sites primarily by olfactory cues, visual concealment might not protect nest from depredation (Holoway 1991). The majority of nest depredation by mammals in northern Florida and southern Georgia was nocturnal (Staller et al. 2005). About 85% of the nest depredations during Rader's (2006) study in Texas were nocturnal (M. J. Rader, Wisconsin Department of Natural Resources, personal communication). Thus, microhabitat variables affecting visual concealment may not be influencing nest depredation because olfactory cues may be used primarily to locate nests.

6. *Nest density (Sugden and Beyersbergen 1987) and the abundance of alternate food items (Colwell 1992) may influence the searching behavior of nest predators.* The density of nests and the abundance of alternate food items may influence the searching behavior of predators (MacArthur and Pianka 1966) and the rate of depredation. Sugden and Beyersbergen (1986, 1987) demonstrated that American crow (*Corvus brachyhynchos*) depredation on artificial duck nests was density dependent, with depredation rates increasing at nest densities greater than 1 nest/ha and reaching an asymptote at densities of 6 nests/ha. Concealment was important where avian predators were dominant (Sugden and Beyersbergen 1986, 1987) but

offered less protection from mammalian predators. To my knowledge, no one has investigated the effect of nest density on depredation rates of northern bobwhites nor has there been any studies looking at the abundance of alternative food items for bobwhite predators. The influence of nest density on the functional response of predators may account for the failure to detect a relationship between microhabitat variables at the nest site and nest fate, however, research is needed to better understand the relationship between bobwhite nest density and nest depredation rates.

7. *Investigator influence on nest fate (Götmark and Åhlund 1984).*

The effect of the researcher locating the radio-marked, incubating bird may have biased the nesting outcome regardless of the microhabitat variables at the nest site. Human scent may repel, attract, or have neutral effects on the depredation rates of mammalian predators (Donalty and Henke 2001). Some studies have demonstrated an observer disturbance effect on nest success, while others report little or no effect (Evans and Wolfe 1967, Bart 1978, Ellison and Cleary 1978, Gottfried and Thompson 1978, Ollason and Dunnet 1980, and Strang 1980). Donalty and Henke (2001) detected no difference in depredation rates of simulated bobwhite nests among human scent masked by a neutralizing agent, human scent masked by dog scent, and human scent as a control. Predators that use olfaction as their primary means to locate prey were capable of locating simulated nests despite attempts to conceal the observers scent trail (Donalty and Henke 2001). Because my nests

where located and monitored in the same manner throughout the study, however, any biases from observers where equal among all nests.

8. *Parental activity at nest-sites may have attracted certain predators (Roper and Goldstein 1997).*

   Little is known about the behaviors or time budgets of nesting bobwhites (Smith 2003). Smith (2003) viewed videotapes from bobwhite nests to obtain 24,677 nesting behavior samples from 35 nesting attempts in the Texas panhandle. Documented behaviors of the incubating bobwhites included gular flutter, turning of eggs, movements to and from the nest, and additional unique behaviors. Rare behaviors included pecking at the nest, pecking out of the nest, calling from the nest, and defensive behavior towards the camera. It is possible that behavioral activity could have attracted predators. However, Smith (2003) reported that sleeping and sitting were the dominant behaviors of nesting bobwhites in the Texas panhandle accounting for >61% of the nesting behavior samples. Thus, it is doubtful that incubating behavior influenced predation risk.

In summary, research does not appear to support the nest-concealment hypothesis for northern bobwhites. On my study site, nest predation appears to be a random process but the generality of this result warrants further testing.

MANAGEMENT IMPLICATIONS

The observation that bobwhite nest depredation may occur in a random fashion on my study area precludes a solution based on habitat management. Predator density, alternate prey, ecosystem processes, and landscape features are all plausible factors influencing

nest depredation from a holistic standpoint that can be manipulated within a management context. My results provide indirect support for the usable space hypothesis (Guthery 1997, 2002:150) which suggests that mean bobwhite density is a function of quantity of usable space rather than quality. Managers therefore should manage for amount of adequate nesting cover and not habitat with specific nest-fate attributes. Thus, to increase bobwhite populations by influencing nest production, managers should manage for increasing the amount of adequate nesting cover (Arredondo et al. 2007, Rader et al. 2007) and not habitat with specific nest-fate attributes (quality).

CHAPTER III

A RADIO-TELEMETRY BASED SIMULATION MODEL FOR NORTHERN BOBWHITES IN SOUTHERN TEXAS

Northern bobwhite populations are complex, dynamic systems whose biotic components (i.e., population and habitat parameters) are intricately interrelated with its abiotic ones (i.e., weather) (Roseberry and Klimstra 1984). Southwestern quail populations are well known for their dynamic nature that is heavily influenced by weather (Heffelfinger et al. 1999, Guthery et al. 2000*c*, Bridges et al. 2001, Guthery et al. 2001, Perez et al. 2002, Hernández et al. 2005). Populations in these semi-arid rangelands have been described as an "unstable utopia" (Lehmann 1984:3–7) and a "boom and bust" phenomenon. Annual surveys conducted both at the state and national scale (e.g., North American Breeding Bird Survey) exhibit this irruptive nature of the species (Fig. 3.1; DeMaso et al. 2002), and recent research has documented a pronounced cyclic behavior which is synchronized by wet-dry cycles (Lusk et al. (2007).

The complex nature of bobwhite populations lends itself to a modeling approach to gain a better understanding their dynamic behavior. Models are formal descriptions of a real system and are useful for investigating and understanding complex, dynamic systems (Grant et al. 1997:18). Northern bobwhites represent an extensively studied species for which a broad knowledge base exists (Guthery 2002:3–8, Sandercock et al. 2008). Surprisingly, population models for northern bobwhite are virtually non-existent, except for 2 notable exceptions: Roseberry and Klimstra (1984) and Guthery et al.

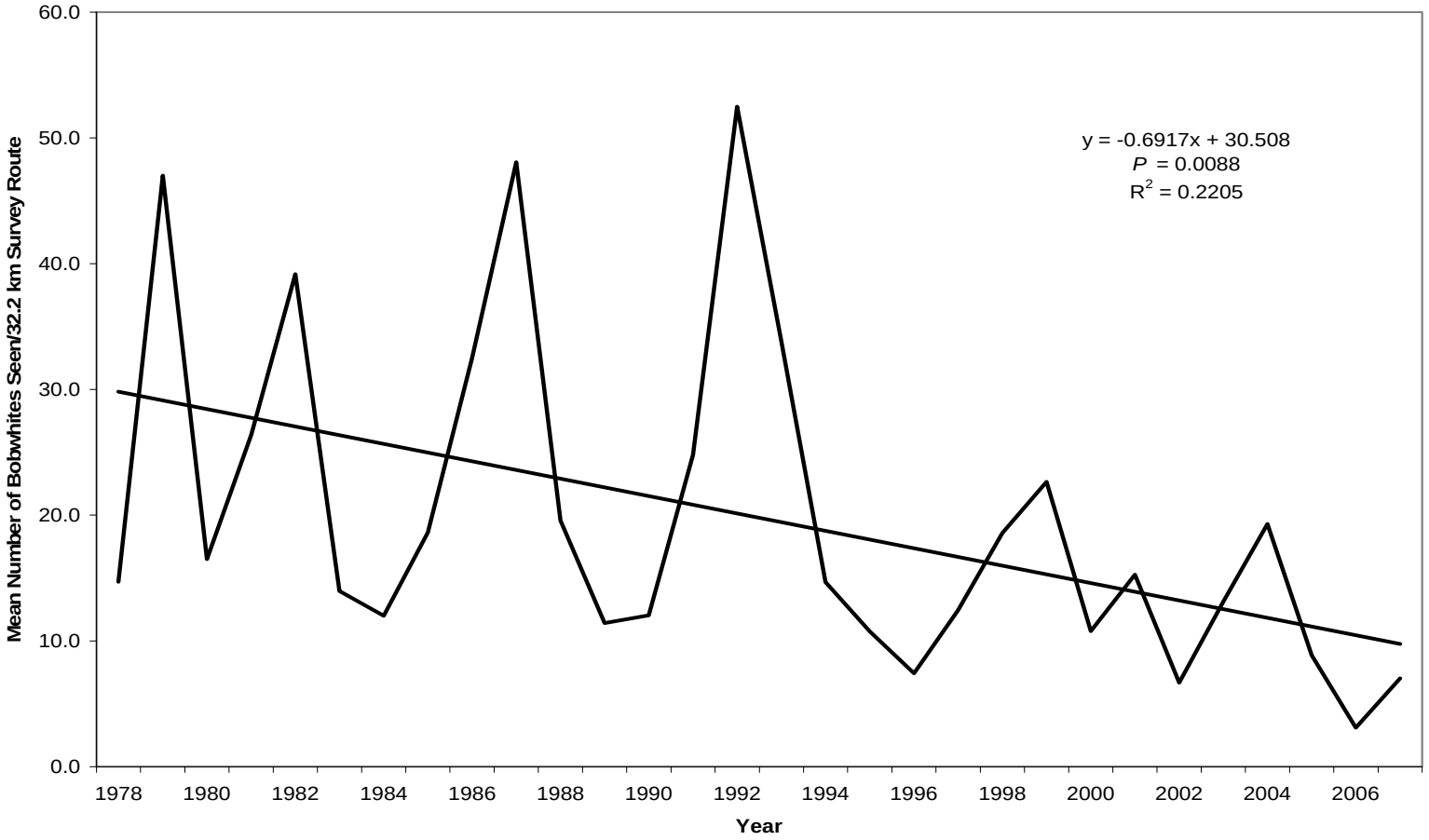

Figure 3.1. Texas Parks and Wildlife Department's August bobwhite roadside survey (mean number of bobwhites seen/32.2 km survey route) trend and fluctuations, south Texas, 1978–2007 (TPWD 2008).

(2000*a*). The former, however, was never compiled into a unified population model and the latter was not age- or sex-structured. Unstructured population models facilitate the modeling process but fail to examine the underlying demographic parameters on population dynamics (Sandercock et al. 2008). Demographic differences are known to exist between ages and sexes in bobwhites (Robel 1965, Pollock et al. 1989*a*, Palmer and Wellendorf 2007, Terhune et al. 2007) and therefore would be important factors to consider when developing a population model for the species.

My goal was to develop an age-, sex-structured population model for northern bobwhite to gain a better understanding of their population dynamics. Because radiotelemetry has been implicated as a potential source of negative bias in bobwhite survival estimates (Guthery and Lusk 2004), such a model also would be useful in evaluating the validity of such concern through population viability analyses using telemetry-based data. Therefore, the objectives of my study were to 1) develop a unified age- and sex-structured population model for northern bobwhite, 2) evaluate model performance by comparing simulation results with empirical estimates of 8 demographic parameters (female- and male-adult annual survival, fall and spring density, fall and spring population size [λ], and winter age ratios), 3) determine which demographic variable(s) exerted the greatest influence on population dynamics via a sensitivity analysis, and 4) indirectly evaluate the validity of radio-telemetry survival estimates by determining the probability of population persistence for 100 years using telemetry-derived estimates of survival.

STUDY AREA

The study area is located on a private hunting lease on the Encino Division of King Ranch, Brooks County, Texas which lies within the Rio Grande Plains ecoregion (Gould 1975). The study area consisted of 3 spatially-independent experimental units (i.e., pastures): North Viboras (1,966 ha), La Loba (1,379 ha), and Cuates (1,240 ha). Experimental units were arranged north to south, respectively, and were separated by ~5 km from each other. A woody cover gradient occurred from north to south, with woody cover decreasing on a southerly gradient. Woody canopy cover was >30% (North Viboras), ~25% (La Loba), and ~10% (Cuates) (Rusk 2006).

Vegetation in the Rio Grande Plains ecoregion is characterized as a mixed-brush community (Scifres 1980:30). Vegetation specific to the study area consisted predominantly of honey mesquite (*Prosopis glandulosa*), huisache (*Acacia smallii*), granjeno (*Celtis pallida*), live oak (*Quercus virginiana*), and pricklypear cactus (*Optuntia lindheimeri*) (Hernández et al. 2002). Predominant forbs included croton (*Croton* spp.), sunflower (*Helianthus annuus*), dayflower (*Commelina erecta*), and partridge pea (*Chamaecrista fasciculata*) (Hernández et al. 2002). Common grasses included little bluestem (*Schizachyrium scoparium*), paspalum (*Paspalum* spp.), three awn (*Aristida* spp.), gulf cordgrass (*Spartina spartinae*), King Ranch bluestem (*Bothriochloa ischaemum*), Kleberg bluestem (*Dichanthium annulatum*), sandbur (*Cenchrus incertus*), red lovegrass (*Eragrostis secundiflora*), and buffelgrass (*Pennisetum ciliare*) (Hernández et al. 2002).

Climatic conditions are classified as semi-arid, sub-humid and are characterized by a high rate of evaporation (Williamson 1983). The months of June and September receive the greatest amount of precipitation. Monthly precipitation ranges from 1.4–13.0 cm with a mean annual rainfall of 65.4 cm (Williamson 1983). The 33-year mean temperature is 22.3 C (range 13.1–29.8 C). January is the coldest month ($\bar{x}$ = 13.1 C), and July is the hottest month ($\bar{x}$ = 29.8 C) (Williamson 1983).

METHODS

Data Sources of Demographic Parameters

The collection of telemetry data was focused on an 800-ha square area centered within each experimental unit. I captured bobwhites using standard funnel traps (Stoddard 1931:442) and night-netting (Labisky 1968) year-round during 1999–2005. Individuals were classified by sex and age (Rosene 1969:44–54), leg-banded, and birds weighing ≥150 g were fitted with a 5–6 g neck-loop radio transmitter (Shields et al. 1982) (American Wildlife Enterprises, Tallahassee, Florida, USA). Radio-marked bobwhites were located >2 weekly and >3/week during the nesting season (Apr–Oct). Bobwhites were monitored throughout the year which was partitioned into 4 seasons based on bobwhite life history: breeding (Season 2; 1 Mar–31 May), nesting (Season 3; 1 Jun–31 Aug), covey pre-frost (Season 4; 1 Sep–30 Nov), and covey post-frost (Season 1; 1 Dec–28 Feb).

Survival data.—Survival rates were calculated using the Kaplan-Meier estimator (Kaplan and Meier 1958) and staggered-entry approach (Pollock et al. 1989*b*, Pollock 1989*c*) to estimate seasonal survival. I assumed that birds were randomly sampled,

survival times for individuals were independent, left-censored individuals (staggered entry) had survival distributions similar to previously marked individuals, and causes for censoring (i.e., radio failure) were independent of the birds fate. I only included bobwhites surviving >14 days after radio-marking to minimize trapping or handling bias on survival probabilities (Pollock et al. 1989*b*, Pollock et al. 1989*c*, White and Garrott 1990).

Nesting data.—I used radio-marked bobwhites to estimate the proportion of hens that entered the nesting season (15 Apr) and attempted to nest, regardless of the nest fate and regardless if hens survived the nesting season. I assumed nesting when I obtained consecutive locations of a radio-marked bird at the same point and located nests by homing. When a nest was found, I continued monitoring until nesting was terminated (i.e., abandoned, depredated, or hatched). I also used these hens to determine the number of nesting attempts per hen, because I had complete nesting histories for each hen entering the nesting season. Once a nest was terminated, I estimated clutch size. I determined the frequency of nesting attempts during the spring (season = 2) and summer (season = 3) regardless of their nest fate.

Density.—Rusk et al. (2007) evaluated survey methods for estimating bobwhite density on my study area using distance sampling (Buckland et al. 2001). Transects were developed in ArcMap and uploaded onto field computers so survey effort and detections could be monitored in the field to determine if the necessary sample size (i.e., >60 detections) and effort (i.e., 91-km of effort) was accrued. The number and length of transects varied per pasture because of the shape of the pasture perimeter. Transects

were traversed during the first and/or last 3 hours of daylight. Transects were flown at a height of 7 m and a velocity of 37 km/hr using a Robinson R44 (Robinson Helicopter Company, Torrance, California). Pilots utilized an Envizio plus lightbar (Raven Industries, Sioux Falls, South Dakota) to navigate transects. The recorded perpendicular distances were analyzed with Program DISTANCE 5.0 (Thomas et al. 2004). The best detection function was chosen based on Akaike's Informatin Criterion (AIC) values and goodness of fit using Chi-square analysis (Buckland et al. 2001). Starting transects were randomly selected by randomly selecting a transect and flying the subsequent transect that was 400-m away. I continued with this scheme in a sequential manner until all transects were traversed.

I used density estimates derived from helicopter transects for fall (Oct–Dec 2005–2007) and spring (Mar 2007–2008) (Rusk et al. 2007, M. J. Schnupp, Caesar Kleberg Wildlife Research Institute, unpublished data) to evaluate the performance of my simulation model. These data were independent from the model and used to evaluate the model performance.

Age ratio.—Winter age ratios (juveniles:adult) where based on hunter harvested birds (1983–2007) from a commercial hunting camp on the study area. This data also were independent from the model and used to evaluate the model performance.

Juvenile spring and summer mortality.—I did not estimate survival of bobwhite chicks (from day 0 to 150) in my study. Estimating survival or mortality of young bobwhites (chicks and juveniles to day 150) is difficult and the rates change from the first few weeks of life to later stages of development (DeMaso et al. 1997). Thus, I used

the daily survival rate (0.9957) reported by Lusk et al. (2005) to estimate chick survival to 150 days.

Bobwhite chick mass at hatch is about 6.6 g and mass gain varies to about 106 days old (Stoddard 1931:72). Lusk et al. (2005) reported that bobwhite growth rate became 0.0 at about 145 days post hatching. During my study, bobwhites needed to weigh 150 g before being radio-marked. Therefore, I used $(0.9957)^{150} = 0.52$ as an estimate of survival during spring and summer. Juvenile mortality for both sexes during spring and summer was $1 – 0.52 = 0.48$.

Model Overview

The model represented production and survival of adult and juvenile, female and male radio-marked bobwhites on an 800–ha study area in the Rio Grande Plains (Fig. 3.2 and Appendix A). Chicks produced during seasons 2 and 3 were separated into female and male juvenile segments of the population. Seasonal mortality was removed from each segment of the population (female juvenile, female adult, male juvenile, male adult). The juvenile cohorts entered the adult cohort in season 1 and remain there throughout their lifetime. Egress and ingress were assumed to be equal (Guthery 2002:45).

I included density-dependent mortality (Roseberry and Klimstra 1984:54) and density-dependent production (Errington 1945, Cookingham and Ripley 1964, Roseberry and Klimstra 1984:96) in my model. There is little doubt that density-dependent effects occur in bobwhite populations, but the nature of the functional relationship between density and population variables remains unclear (Guthery et al. 2000*a*). Data collected via radio telemetry during 2000–2005 were used to estimate demographic parameters and their Weibull distributions (See the Variable Distributions to Invoke Stochasticity section below). Variables were randomly drawn from these distributions to give the model stochasticity.

Description of the conceptual model.—The model was developed using STELLA® 9.0.2 software (ISEE Systems, Incorporated, Lebanon, New Hampshire, USA). It was based on difference equations where Δt = 3 months with stochastic variables randomly drawn from their Weibull distributions. I ran simulations for 100 years and evaluated model output by comparing predicted annual survival for adult bobwhites, fall and spring density, λ in the fall population, and winter age ratios

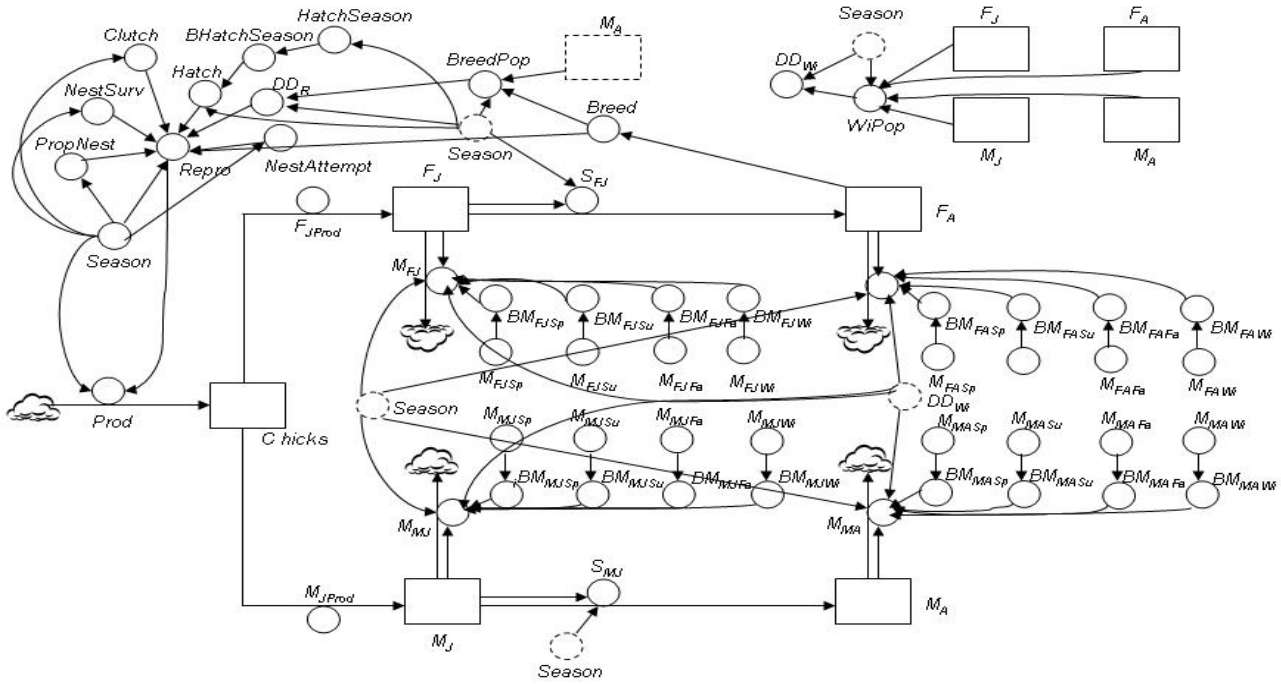

Figure 3.2. Conceptual diagram of a northern bobwhite population model for the Rio Grande Plains, Texas. Boxes indicate state variables (stocks), circles indicate driving variables, constants, or auxiliary variables, and arrows going from a state variable to another state variable with a circle touching the arrow are material transfers.

(juvenile:adult) to observed data from the field.

Variable distributions to invoke stochasticity.—Stochastic models would have variables randomly drawn from their probability distribution functions. Often, probability distribution functions are not available from empirical data for modeling purposes and are assumed to be normally distributed (Guthery et al. 2000*a*) which is a tenuous assumption when dealing with biological and ecological data (Young and Young 1998). I used a Weibull distribution to characterize bobwhite demographic variables estimated from data collected using radio-marked bobwhites on my study areas. I chose the Weibull distribution because it's flexibility to mimic many statistical distributions (Smith and Naylor 1987), it's parameters could be easily estimated, and it fit most of my data. The Weibull distribution has 3 parameters: a continuous shape parameter (α), a continuous scale parameter (β), and a continuous location parameter (γ). The distribution will vary in shape depending on the value of these parameters. Parameters for the distribution of each particular demographic variable were estimated with SAS software using the histogram statement and Weibull option in PROC UNIVARIATE (SAS Institute, Incorporated, 2006).

STELLA® software draws from the Weibull distribution using the method of inversion (Naylor et al. 1966:70–73). Weibull parameters (Appendix B) were used in the following formula

$$\text{Weibull} = \beta * (-\text{LOGN}(\text{RANDOM}(0,1))^{(1/\alpha)} + \gamma \text{ , (STELLA® 9.0.2).}$$

For example, mortality would be calculated as

Mortality = 1 – (β * (-LOGN(RANDOM(0,1))$^{(1/\alpha)}$ + γ),

because the Weibull distribution is for survival.

Model variables using the Weibull distribution to invoke stochasticity included: clutch size (*Clutch*), the proportion of adult female bobwhites that entered the nesting season and nested during the spring and/or the summer (*PropNest*), the number of nesting attempts per adult female that entered the nesting season and nested during that nesting season (*NestAttempt*), female, juvenile fall and winter mortality (M_{FJFa}; M_{FJWi}), male, juvenile fall and winter mortality (M_{MJFa}; M_{MJWi}), female, adult mortality during spring, summer, and winter (M_{FASp}; M_{FASu}; M_{FAWi}), and male, adult mortality during spring, fall, and winter (M_{MASp}; M_{MAFa}; M_{MAWi}).

Normal distributions were used for the proportion of nests hatched during the spring and summer season (*Hatch*) ($\bar{x}$ = 0.261, SD = 0.225); female, adult fall mortality (M_{FAFa}) ($\bar{x}$ = 0.720, SD = 0.187); and male, adult summer mortality (M_{MASu}) ($\bar{x}$ = 0.586, SD = 0.157) because ≥1 Weibull parameter could not be estimated. Distributions were bounded by the minimum and maximum variable estimate from the field data. STELLA® software draws from the normal distribution using the mean ($\bar{x}$) and standard deviation (SD) (Appendix 3) in the following formula:

NORMAL($\bar{x}$, SD), (STELLA® 9.0.2).

Therefore, mortality would be calculated as

Mortality = (1 – NORMAL($\bar{x}$, SD)),

because survival was assumed to be normally distributed.

Baseline simulations.—The primary use of the model was to better understand bobwhite demography in southern latitudes and to determine if the population could persist based on demographic estimates derived from radio-telemetry data. I was particularly interested in the fall and spring populations because the fall population represents the population subjected to harvest and the spring population represents the breeding population. Bobwhite hunting is economically important to many south Texas communities (Connor 2007), and the spring population is important to population persistence (Guthery et al. 2002). My reference value for determining population changes was to detect a true difference of 250 individuals in the fall or spring populations at a significance level of $\alpha = 0.05$ with a probability of $P = 0.80$ that the difference would be detected if it existed (Grant et al. 1997). I estimated the number of simulations to run (n) using the formula provided by Sokal and Rohlf (1969:247) and Grant et al. (1997:62–63) using the variance estimates above to calculate the standard deviations of the fall and spring populations. I conducted 50 preliminary stochastic baseline simulations to obtain variance estimates and calculate required sample sizes. This exercise yielded the following variance estimates and required sample sizes:

fall density (variance = 0.07; $n = 50$),

fall population (variance = 279,218.00; $n = 75$),

spring density (variance = 0.10, $n = 75$),

spring population (variance = 462,056.50; $n = 120$)

female adult annual survival (variance = 0.008; $n = 55$),

male adult annual survival (variance = 0.004; $n = 30$), and

winter age ratio (juvenile:adult) (variance = 5.90; $n = 100$).

Based on these results, I decided to conduct 120 simulations because it was the largest number of simulations suggested by my required sample size calculations.

Quantitative Description of the Model

Verbal descriptions of model variables and parameters are detailed in appendix A. The model is based on difference equations ($\Delta t = 3$ months), was programmed using STELLA® 9.0.2 software (ISEE Systems, Incorporated, Lebanon, New Hampshire, USA), and includes 5 state variables (1.0–5.0), including the number of chicks ($Chicks_{(t)}$), juvenile females ($F_{J(t)}$), juvenile males ($M_{J(t)}$), adult females ($F_{A(t)}$), and adult males ($M_{A(t)}$) in the population at the beginning of time t.

$$Chicks_{(t+1)} = Chicks_{(t)} + (Prod_{(t)} - F_{JProd(t)} - M_{JProd(t)}) * \Delta t \qquad (1.0)$$

The initial value for $Chicks_{(t)}$ is 500. $Prod_{(t)}$ represents the number of chicks entering the system during time t that survive to the end of that time interval, that is, the net recruitment of chicks during time t. $F_{JProd(t)}$ and $M_{JProd(t)}$ represent the number of female and male chicks, respectively, that survive to become juveniles (at 3 months of age) during time t. The sex ratio (females:males) at hatch is 50:50 (Rosene 1969:186, Lusk et al. 2005), thus:

$$F_{JProd(t)} = M_{JProd(t)} = Chicks_{(t)} * 0.5$$

$$Prod_{(t)} = BHatchSeason_{(t)} * F_{A(t)} * Clutch_{(t)} * NestSurv_{(t)} * NestAttempt_{(t)} * PropNest_{(t)} * DD_{R(t)}, \text{ if } Season = 2 \text{ or } Season = 3$$

$$Prod_{(t)} = 0, \text{ if } Season = 1 \text{ or } Season = 4$$

where *Season* is an index that is assigned the values 1, 2, 3, and 4 sequentially throughout the simulation, representing winter, spring, summer, and fall seasons, respectively. $BHatchSeason_{(t)}$ represents the proportion of nests that hatch during time *t*. During spring (*Season* = 2), the value of $BHatchSeason_{(t)}$ is randomly drawn from normal distribution, truncated at 0.0 and 1.0, with a mean (SD) of 0.26 (0.23). During summer (*Season* = 3), the value of $BHatchSeason_{(t)}$ is equal to one minus its value the preceding spring. $Clutch_{(t)}$ is the clutch size (randomly drawn from Weibull distribution) during time *t*, $NestSurv_{(t)}$ is the estimate of daily nest survival (0.9593) from Radar et al. (2007), raised to the 23 power to estimate nest survival for the 23-day incubation period (constant) during time *t*, $NestAttempt_{(t)}$ is the number of nesting attempts per adult female during time t (randomly drawn from Weibull distribution), and $PropNest_{(t)}$ is the proportion of females that nest during time t (randomly drawn from Weibull distribution).

$DD_{R(t)}$ represents the density-dependent relationship between population size (adults only) and production:

$DD_{R(t)} = (-0.0004 * (F_{A(t)} + M_{A(t)})) + 0.9525$, if *Season* = 2 or *Season* = 3

$DD_{R(t)} = 0$, if *Season* = 1 or *Season = 4*

Female Juveniles ($F_{J(t)}$).

$$F_{J(t+1)} = F_{J(t)} + (F_{JProd(t)} - M_{FJ(t)} - S_{FJ(t)}) * \Delta t \qquad (2.0)$$

where $M_{FJ(t)}$ represents the number of juvenile females dying during time *t*.

$M_{FJ(t)} = MRate_{FJ(t)} * F_{J(t)} * DD_{Wi}$

where $MRate_{FJ(t)}$ is the female juvenile mortality rate, which depends on the season (if *Season* = 1 then M_{FJWi}; if *Season* = 2 then M_{FJSp}; if *Season* = 3 then M_{FJSu}; if *Season* = 4 then M_{FJFa};) is drawn randomly from a Weibull distribution (parameters for the Weibull distribution are given in Appendix B), truncated at 0.0 and 1.0, if *Season* = 1, is drawn randomly from a Weibull distribution (parameters for the Weibull distribution are given in Appendix B), truncated at 0.0 and 0.45, if *Season* = 4, and is equal to 0.48 if *Season* = 2 or *Season* = 3. DD_{Wi} represents the density-dependent relationship between population size (juveniles and adults only) and winter mortality:

$$DD_{Wi} = (0.0004 * (F_A + F_J + M_A + M_J)) + 0.0950, \text{ if } Season = 1$$

and $M_{FJ(t)} = MRate_{FJ(t)} * F_{J(t)}$, if *Season* > 1.

$S_{FJ(t)}$ represents juvenile females that survive to become adults during time t.

$S_{FJ(t)} = F_{J(t)} - M_{FJ(t)}$ if *Season* = 1

$S_{FJ(t)} = 0$ if *Season* > 1

Female Adults ($F_{A(t+1)}$).

$$F_{A(t+1)} = F_{A(t)} + (S_{FJ(t)} - M_{FA(t)}) * \Delta t \qquad (3.0)$$

where $M_{FA(t)}$ represents the number of adult females dying during time *t*.

$$M_{FA(t)} = MRate_{FA(t)} * F_{A(t)} * DD_{Wi},$$

where $MRate_{FA(t)}$ is the female adult mortality rate, which depends on the season (if *Season* = 1 then M_{FAWi}; if *Season* = 2 then M_{FASp}; if *Season* = 3 then M_{FASu}; if *Season* = 4 then M_{FAFa}) and is drawn randomly from a Weibull distribution (parameters for the Weibull distribution are given in Appendix B), truncated at 0.0 and 0.75 if *Season* = 1, 0.0 and 0.8, *Season* = 2, and 0.0 and 0.78 *Season* = 3. If *Season* = 4, $MRate_{FA(t)}$ is

drawn randomly from a normal distribution, truncated at 0.0 and 0.57, with a mean (SD) of 0.72 (0.19).

Male Juveniles ($M_{J(t)}$).

$$M_{J(t+1)} = M_{J(t)} + (M_{JProd(t)} - M_{MJ(t)} - S_{MJ(t)}) * \Delta t \quad (4.0)$$

where $M_{MJ(t)}$ represents the number of juvenile males dying during time *t*.

$$M_{MJ(t)} = MRate_{MJ(t)} * F_{M(t)} * DD_{Wi},$$

where $MRate_{MJ(t)}$ is the male juvenile mortality rate, which depends on the season (if *Season* = 1 then M_{MJWi}; if *Season* = 2 then M_{MJSp}; if *Season* = 3 then M_{MJSu}; if *Season* = 4 then M_{FJFa}) and is drawn randomly from a Weibull distribution (parameters for the Weibull distribution are given in Appendix B), truncated at 0.0 and 1.0, if *Season* = 1, is drawn randomly from a Weibull distribution (parameters for the Weibull distribution are given in Appendix B), truncated at 0.0 and 0.20, if *Season* = 4, and is equal to 0.48 if *Season* = 2 or *Season* = 3.

$S_{MJ(t)}$ represents juvenile males that survive to become adults during time *t*.

$S_{MJ(t)} = M_{J(t)} - M_{MJ(t)}$ if *Season* = 1

$S_{MJ(t)} = 0$ if *Season* > 1

Male Adults ($M_{A(t)}$).

$$M_{A(t+1)} = M_{A(t)} + (S_{MJ(t)} - M_{MA(t)}) * \Delta t \quad (5.0)$$

where $M_{MA(t)}$ represents the number of adult males dying during time *t*.

$$M_{MA(t)} = MRate_{MA(t)} * M_{A(t)} * DD_{Wi}$$

where $MRate_{MA(t)}$ is the male adult mortality rate, which depends on the season (if *Season* = 1 then M_{MAWi}; if *Season* = 2 then M_{MASp}; if *Season* = 3 then M_{MASu}; if *Season* =

4 then M_{MAFa}) and is drawn randomly from a Weibull distribution (parameters for the Weibull distribution are given in Appendix B), truncated at 0.0 and 1.0 if *Season* = 1, 0.0 and 0.7, *Season* = 2, and 0.0 and 0.43 *Season* = 4. If *Season* = 3, $MRate_{MA(t)}$ is drawn randomly from a normal distribution, truncated at 0.18 and 0.82, with a mean (SD) of 0.59 (0.16).

Model Verification and Evaluation

I solved the equations to 1 time step and compared my calculations to those of the simulation model to ensure that various mathematical equations in the model functioned as intended. Similar results indicated the model was performing properly. Once the model calculations were verified, I evaluated model performance by:

1. Visually evaluating population trends of model output for population fluctuations characteristic of the species previously reported (i.e., "boom-and-bust" phenomenon and population fluctuations around a demographic capacity);
2. Comparing the population trend and slope of my simulation model to an independent population index, Texas Parks and Wildlife Department (TPWD) August roadside counts, using linear regression;
3. Verifying density-dependent effects in model output given density-dependent reproduction and winter mortality were built into the model;
4. Comparing model predictions of 6 demographic parameters (female- and male-adult annual survival, fall and spring density, finite rate of increase [λ], and winter age ratios) obtained from 120 replicate-stochastic simulations to field data from the study area; and

5. Comparing model predictions of 6 demographic parameters listed above to values for those parameters reported in the literature.

I used 95% confidence intervals for univariate comparisons between variables predicted from the simulation model and observed values from field data (Johnson 1999).

Sensitivity Analysis

Sensitivity analysis is a technique used in model evaluation to determine the sensitivity of model output to particular model parameters (Grant et al. 1997:81). Selected parameter values are varied one at a time by a specific amount, and the simulation is compared to baseline results. To perform the sensitivity analysis, I converted my stochastic bobwhite population model to a deterministic model by replacing the Weibull distributions with the mean parameter estimates (Table 3.1). I performed the sensitivity analysis by varying the mean value of 25 model parameters by +35% and –35% to determine the sensitivity of the fall population to their variation (Table 3.1). The choice of the variation (i.e., ±35%) was based on the mean variation associated with the parameter estimates. For example, if the baseline (mean value) for nesting attempts/hen

Table 3.1. Sample size (n), mean ($\bar{x}$), and 95% confidence interval (CI) for 25 model parameters used in the northern bobwhite population model sensitivity analysis.

Category Parameter	n	$\bar{x}$	Lower 95% CI	Upper 95% CI
Density dependence				
Winter mortality[a]		0.0004		
Reproduction[a]		–0.0004		
Mortality				
Female adult spring	15	0.456	0.340	0.573
Female adult summer	15	0.388	0.281	0.496
Female adult fall	15	0.280	0.176	0.383
Female adult winter	15	0.326	0.172	0.479
Female juvenile spring[b]		0.476		
Female juvenile summer[b]		0.476		
Female juvenile fall	5	0.033	0.000	0.126
Female juvenile winter	12	0.354	0.123	0.585
Male adult spring	15	0.384	0.286	0.482
Male adult summer	15	0.415	0.327	0.502
Male adult fall	15	0.187	0.121	0.254
Male adult winter	15	0.462	0.309	0.615
Male juvenile spring[b]		0.476		
Male juvenile summer[b]		0.476		

Table 3.1. Continued.

Parameter	n	$\bar{x}$	Lower 95% CI	Upper 95% CI
Category				
Male juvenile fall	7	0.057	0.000	0.147
Male juvenile winter	10	0.432	0.189	0.675
Productivity				
Sex ratio at hatch				
Female[c]		0.500		
Male[c]		0.500		
Nesting attempts/hen	15	1.7	1.4	2.0
Nest survival[d]		0.385	0.290	0.509
Proportion hens nesting	15	0.656	0.574	0.739
% nest per season				
Spring	15	0.261	0.137	0.386
Summer	15	0.673	0.516	0.829

[a]Slope of the theoretical, linear relationship between winter mortality and winter population and reproduction and spring and summer populations. Therefore, no estimate of variance is associated with the intercept and slope of the regression line.

[b]Estimates derived from data in Lusk et al. (2005).

[c]Estimates from Collier et al. (2007).

[d]Estimates derived from data in Rader et al. (2007) for 23-day incubation period.

is 1.7, then the -35% value = 1.1 and the +35% value = 2.3. These values would then be used in the sensitivity analysis. I did not include female-juvenile fall mortality and male-juvenile fall mortality in the sensitivity analysis because of the large amount of variation associated with these estimates. Also, I was more interested in the process variation that model parameters had on the fall population rather than the sampling variation associated with parameter estimates.

Rather than using every model parameter in the sensitivity analysis, I selected model parameters for the sensitivity analysis based on reports in the literature about their influence on bobwhite demographics. Below is a brief justification for including the model parameters in the sensitivity analysis I performed. They are grouped into 3 categories; density dependence, survival, and production.

Density dependence.—Evidence suggests that density dependence modifies bobwhite population at certain times and places (Errington 1945, Cookingham and Ripley 1964, Roseberry and Klimstra 1984:96–98, Guthery 2002:54). Many models could be used to describe the relationship between percent summer gain and breeding density (Guthery 2002:56). The strength of density-dependent processes in reproduction varies among species of quail and among populations with species at least within a 10 to 30 year time-frame (Guthery 2002:59). Guthery et al. (2000*a*) hypothesized that the variation in the strength of density dependence varied between northern and southern latitude bobwhite populations and was stronger in northern populations.

Survival.—Wild bobwhites have high mortality rates and mortality is the compliment of survival. Guthery and Lusk (2004) examined 58 bobwhite survival rates

reported in the literature and found 83% of the estimates to be biologically unreasonable (annual survival ≤7 percent). Fall populations consist of bobwhites surviving from the previous year plus the chicks that those bobwhites produce. Because of the bobwhite's life history traits, one would expect that production would have a larger impact on fall populations, rather than survival since bobwhites have short life spans (i.e., 6−8 months; Guthery 2000:119). Since estimates of bobwhite survival vary by age and sex (Robel 1965, Pollock et al. 1989*a*, Palmer and Wellendorf 2007, Terhune et al. 2007), I did not vary and parameters in tandem.

Production.—Production is a key parameter contributing to fall bobwhite populations. Many variables contribute to bobwhite production. Deviations from parity (1:1 sex ratio) are frequent in many avian species (Hardy 1997). Little information exists concerning the sex ratio at hatch for many avian species because of difficulty in differentiating sexes based on phenotypic traits. Collier et al. (2006) reported that Rio Grande wild turkey (*Meleagris gallopavo intermedia*) brood–sex ratios in Texas were similar to parity, but variation in brood–sex ratios caused differences in mean population growth rates in a population model. Since bobwhites and Rio Grande wild turkeys are members of the family *Phasianidae* (Schroger 1966, Johnsgard 1973), even though their annual survival rates differ (bobwhites 0.2–0.3 [Guthery 2002], Rio Grande Wild Turkeys 0.4–0.6 [Holdstock et al. 2006]) I included brood sex ratio in my sensitivity analysis. Little can be done from a management context to affect brood sex ratio, but having a large influence on the ending fall population might indicate an imprecise estimate of brood sex ratios for northern bobwhites.

Bobwhite production is influenced by 4 crucial variables: the proportion of females that lay nests, nesting rate, the probability of nest success, and the number of days in the laying season (Guthery and Kuvlesky 1998, Hernández et al 2005).

Guthery (1997) reports a general latitudinal trend (lower survival and higher production at northern latitudes, higher survival and lower production at southern latitudes) in bobwhite demographics. Hernández et al. (2007) found that productivity and timing of laying was similar between females bobwhites entering their first nesting season and those that had previous nesting experience.

Population Persistence

I used 2 criteria to evaluate population persistence. Guthery et al. (2000*a*) used a quasi-extinction criterion of ≤14 birds which approximated mean covey size reported by Stoddard (1931:170). Their justification for using this criterion was that a covey represented an evolved social unit and was assumed to have adaptive behaviors that influenced fitness. However, population size alone lacks informative value without a reference to area (i.e., density). Thus, I used a quasi-extinction criteria of <0.05 bobwhites/ha (≤40 bobwhites for my study area) based on minimum spring densities reported in the literature (Spears 1991). This criterion is below the 0.25 bobwhites/ha considered to be indicative of very poor bobwhite populations (Guthery 1986:149). I used both of these criteria (≤14 bobwhites and ≤40 bobwhites) to evaluate spring and fall population persistence from the 120 replicate-stochastic simulations conducted above. Spring populations were evaluated because of there importance to production and long-

term population persistence and fall populations were evaluated because of their recreational importance to southern Texas.

RESULTS

Model Evaluation

My model met 5 of the 5 evaluation criteria I set to accept the model as being a reliable model of bobwhite populations in the Rio Grande Plains of Texas. In general, the model performed as expected exhibiting population highs and lows characteristic of northern bobwhite populations in the Rio Grande Plains (Fig. 3.3). Survey data from Texas Parks and Wildlife Department (Fig. 3.1) and the mean of the 5 randomly selected fall population simulations (Fig. 3.4) exhibited a declining trends with similar slopes (95% confidence limits: LCL: -1.20 UCL -0.19, TPWD; LCL -3.09 UCL 0.99, Model). The model also exhibited density-dependent production and tended towards an asymptotic limit (Fig. 3.4). Simulated spring population explained between 25.0 and 33.0% of the variation in the simulated fall population (Fig. 3.5).

Simulated population parameters were similar to those observed in the field for 5 of the 6 population parameters (Table 3.2). Only simulated male adult annual survival ($\bar{x}$ = 0.04, SE = 0.007) differed by 275.0% from field estimates of male adult survival ($\bar{x}$ = 0.15, SE = 0.036) (Table 3.2). In addition, simulated population parameters were similar to those reported in the literature for 6 of the 6 population parameters (Table 3.3).

Sensitivity Analysis

I identified 5 parameters that had the greatest influence (≥22.5% change in the ending fall population) on fall bobwhite populations (Table 3.4). These were nesting

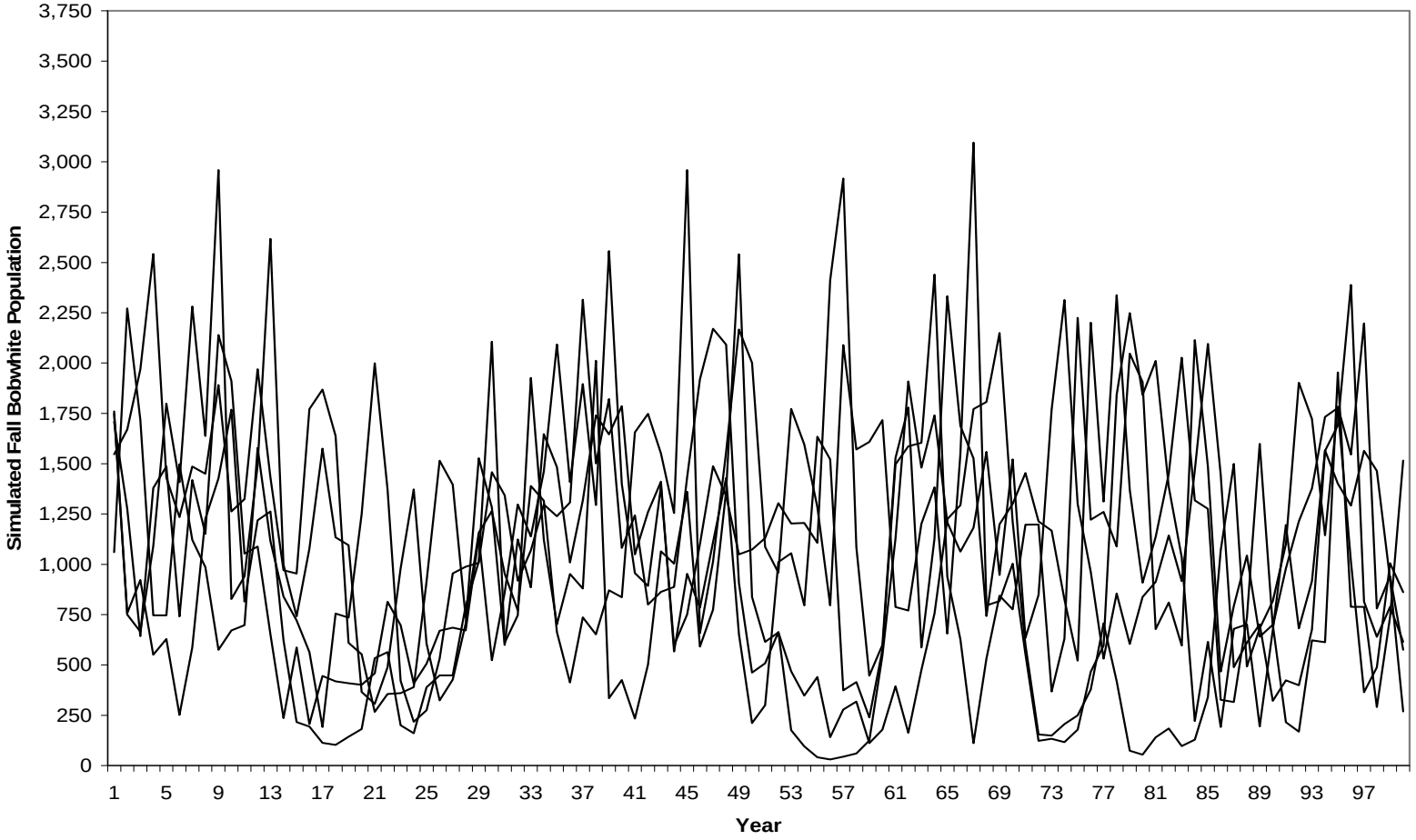

Figure 3.3. Population projections of 5 randomly selected fall bobwhite population simulations of 400 time steps (i.e., 100 years).

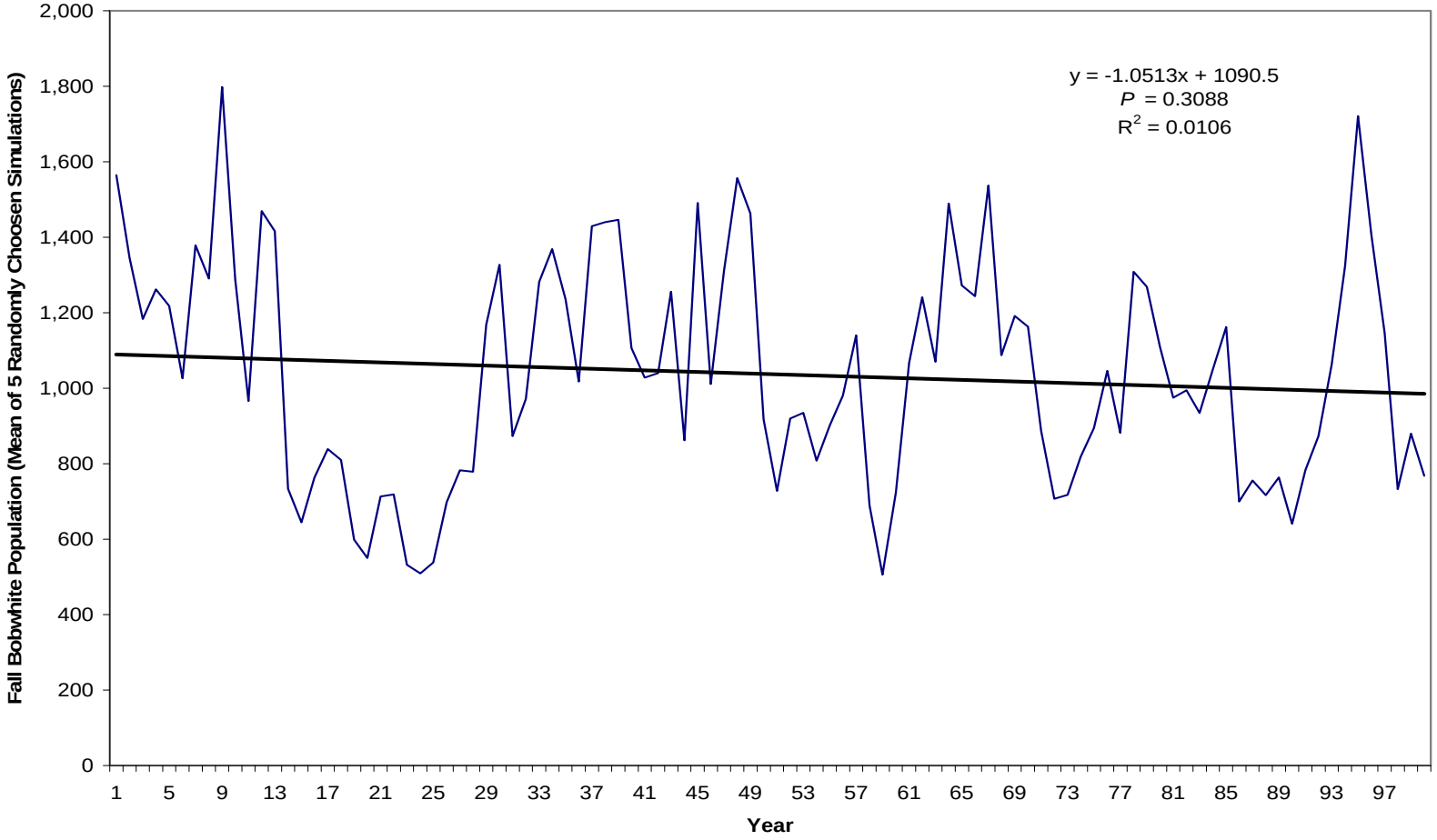

Figure 3.4. Population projection based on the mean of the 5 randomly selected fall bobwhite population simulations in figure 3.3, each simulation 400 time steps (i.e., 100 years).

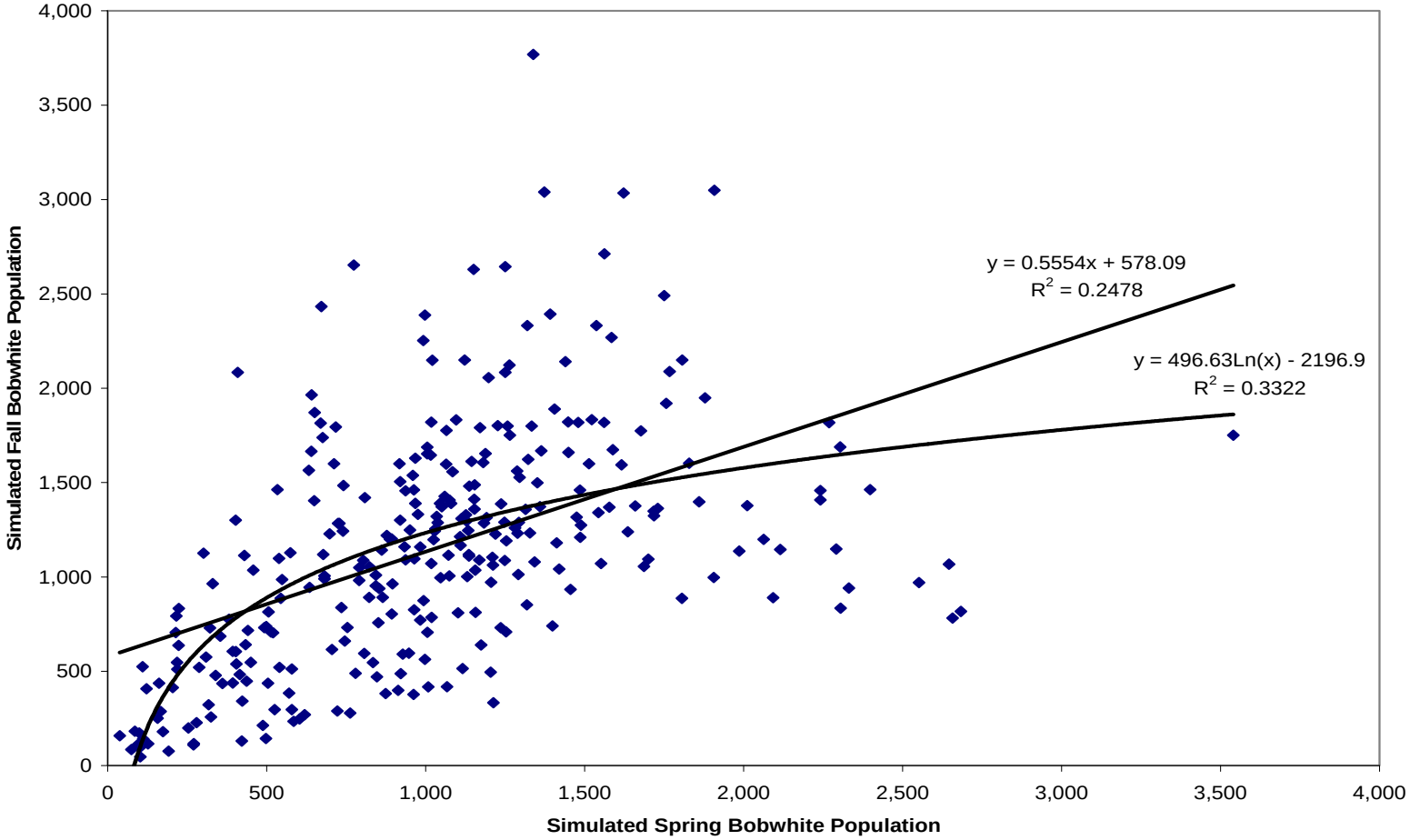

Figure 3.5. Relationship between simulated bobwhite spring population and simulated bobwhite fall population (i.e., population growth).

Table 3.2. Comparisons of 6 demographic parameters between simulated values and observed values of a northern bobwhite population. Observed data was from a bobwhite radio telemetry study conducted from 2001–2005 in Brooks County, Texas, USA.

	Observed						Simulation					
			95% Confidence interval		Range				95% Confidence interval		Range	
Parameter	*n*	$\bar{x}$	Lower	Upper	Min	Max	*n*	$\bar{x}$	Lower	Upper	Min	Max
Annual survival[a]												
Female adult	5	0.14	0.08	0.20	0.04	0.23	120	0.10	0.08	0.12	0.00	0.47
Male adult	5	0.15	0.08	0.22	0.06	0.24	120	0.04	0.03	0.05	0.00	0.58
Density (no./ha)												
Fall	3	1.35	0.45	2.25	0.53	2.13	120	1.25	1.11	1.40	0.03	4.47
Spring	2	1.57	0.00	3.32	0.68	2.47	120	0.99	0.86	1.12	0.03	3.44
Finite rate of increase	2	1.43	0.00	3.74	0.25	2.61	120	1.24	1.11	1.37	0.19	4.14
Juvenile:adult ratio	25	2.85	2.39	3.31	1.06	5.10	120	2.65	2.22	3.07	0.00	11.10

Table 3.2. Continued.

	Observed						Simulation					
			95% Confidence interval		Range				95% Confidence interval		Range	
Parameter	*n*	$\bar{x}$	Lower	Upper	Min	Max	*n*	$\bar{x}$	Lower	Upper	Min	Max

[a]Radio telemetry data were used to estimate seasonal survival (and mortality) on the study area and were used to create the distributions which the simulation model randomly drew estimates. Therefore, the comparisons are not truly independent, but confirm that the distributions work well, at least for female adult bobwhites.

Table 3.3. Comparisons of 6 demographic parameters between simulated values and values reported in the literature for northern bobwhite populations.

	Simulation				Literature			
Parameter	n	$\bar{x}$	Min	Max	Location	Min	Max	Source
Annual survival								
Female adult	120	0.10	0.00	0.47	FL	0.06	0.25	Pollock et al. (1989)[a]
					FL	0.11	0.27	Palmer and Wellendorf (2007)
					GA	0.14	0.40	Terhune et al. (2007)
Male adult	120	0.04	0.00	0.58	FL	0.10	0.30	Pollock et al. (1989)[a]
					FL	0.18	0.38	Palmer and Wellendorf (2007)
					GA	0.15	0.40	Terhune et al. (2007)
Pooled over sexes					OK	0.02	0.21	Cox et al. (2004)
					KS	0.02	0.09	Taylor et al. (1999)[b]
					OK	0.00	0.06	Townsend et al. (1999)[b]
					TX	0.00	0.01	Liu et al. (2000)[b]

Table 3.3. Continued.

Parameter	Simulation				Literature			
	n	$\bar{x}$	Min	Max	Location	Min	Max	Source
					KS	0.00	0.04	Williams et al. (2000)[b]
					KS	0.03	0.16	Williams (2001)[b]
Density (no./ha)								
Fall	120	1.25	0.03	4.47	TX	0.16	4.78	Guthery (1988)
					TX	0.00	2.65	Spears (1991)
					TX	0.19	3.47	Rusk et al. (2007)[c]
					TX	0.27	0.63	Kuvlesky et al. (1989)
Spring	120	0.99	0.03	3.44	TX	0.01	2.18	Guthery (1988)
					TX	0.00	0.32	Spears (1991)
Finite rate of increase	120	1.24	0.19	4.14	WI	0.40	2.30	Errington (1945)
					MA	1.40	2.30	Cookingham and Ripley (1964)
					AL	0.80	1.60	Rosene (1969:Appendix G)

Table 3.3. Continued.

Parameter	Simulation				Literature			
	n	$\bar{x}$	Min	Max	Location	Min	Max	Source
					SC (Groton Plant.)	0.70	1.30	Rosene (1969:Appendix G)
					SC (Friendfield Plant.)	0.70	1.60	Rosene (1969:Appendix G)
					SC (Oakland Club)	0.40	2.00	Rosene (1969:Appendix G)
					TX	0.60	3.10	Rusk et al. (2007)
					TX	0.40	3.20	TPWD (2008)
Juvenile:adult ratio	120	2.65	0.00	11.10	TX	0.60	9.15	Lehmann (1984:133)
					TX	1.70	7.05	Jackson (1969:9)

[a]Annual survival estimates based on band recovery analysis.

[b]From Guthery and Lusk (2004)

[c]Walked and helicopter transects using distance sampling.

Table 3.4. Results of northern bobwhite population model sensitivity analysis of 23 model parameters varied by ±35%, based on variation associated with parameter estimates, if there was a measure of variation associated with the estimate, the absolute difference between the ending fall population at –35% and +35%, and their percent difference from the baseline (mean values for all model parameters) fall population (1,644 birds).

Category Parameter	Variation	Ending fall population	Absolute difference	Percent difference from baseline
Density dependence				
Winter mortality[a]	–35%	1,640	5	–0.24
	+35%	1,645		0.05
Reproduction[a]	–35%	1,260	846	–23.36
	+35%	2,106		28.10
Mortality				
Female adult spring	–35%	1,801	313	9.55
	–35%	1,488		–9.49
Female adult summer	–35%	1,762	236	7.18
	+35%	1,526		–7.18
Female adult fall	–35%	1,683	82	2.37
	+35%	1,601		–2.62
Female adult winter	–35%	1,664	41	1.22
	+35%	1,623		–1.28

Table 3.4. Continued.

Category Parameter	Variation	Ending fall population	Absolute difference	Percent difference from baseline
Female juvenile spring[b]	–35%	1,644	0	0.00
	+35%	1,644		0.00
Female juvenile summer[b]	–35%	1,682	77	2.31
	–35%	1,605		–2.37
Female juvenile fall	–35%	1,653	20	0.55
	+35%	1,633		–0.67
Female juvenile winter	–35%	1,644	0	0.00
	+35%	1,644		0.00
Male adult spring	–35%	1,685	60	2.49
	+35%	1,625		–1.16
Male adult summer	–35%	1,669	49	1.52
	+35%	1,620		–1.46
Male adult fall	–35%	1,631	25	–0.79
	+35%	1,656		0.73
Male adult winter	–35%	1,619	49	–1.52
	+35%	1,668		1.46
Male juvenile spring[b]	–35%	1,644	0	0.00
	+35%	1,644		0.00
Male juvenile summer[b]	–35%	1,644	0	0.00

Table 3.4. Continued.

Category Parameter	Variation	Ending fall population	Absolute difference	Percent difference from baseline
	+35%	1,644		0.00
Male juvenile fall	–35%	1,632	24	–0.73
	+35%	1,656		0.73
Male juvenile winter	–35%	1,644	0	0.00
	+35%	1,644		0.00
Productivity				
Sex ratio at hatch				
Female	–35%	1,123	891	–31.69
	+35%	2,014		22.50
Male	–35%	1,696	52	3.16
	+35%	1,644		0.00
Nesting attempts/hens	–35%	909	1,118	–44.71
	+35%	2,027		23.30
Nest survival[c]	–35%	909	1,119	–44.71
	+35%	2,028		23.36
Proportion hens nesting	–35%	907	1,120	–44.83
	+35%	2,027		23.30
% nest per season				
Spring	–35%	1,601	85	–2.62

Table 3.4. Continued.

Category Parameter	Variation	Ending fall population	Absolute difference	Percent difference from baseline
	+35%	1,686		2.56
Summer	–35%	977	1,018	–40.57
	+35%	1,995		21.35

[a]Slope of the theoretical, linear relationship between winter mortality and winter population and reproduction and spring and summer populations. Therefore, no estimate of variance is associated with the intercept and slope of the regression line.

[b]Estimates derived from data in Lusk et al. (2005).

[c]Estimates derived from data in Rader et al. (2007) for 23-day incubation period.

attempts/hen, nest survival, and proportion of hens nesting, female sex ratio at hatch, and density-dependent reproduction (Table 3.4). Nesting attempts/hen, nest survival, and proportion of hens nesting had the greatest influence on the ending fall population (Table 3.4). Female-juvenile spring mortality, female-juvenile winter mortality, male-juvenile spring mortality, male-juvenile summer mortality, and male-juvenile winter mortality had the least influence on the ending fall population (Table 3.4).

Population Persistence

I used 2 quasi-extinction criteria: my criterion (≤40 birds; ≤0.05 birds/ha) and the criterion of Guthery et al. (2000*a*) (≤14 birds). I documented a probability of population persistence of 74.2% (89 of 120 spring simulations) and 72.5% (87 of 120 fall simulations) for spring and fall, respectively, using the criterion of ≤40 birds. Following the quasi-extinction criterion of Guthery et al. (2000*a*), the probability of persistence was 91.7% (110 of 120 spring simulations) and 91.7% (110 of 120 fall simulations) for the spring and fall population, respectively. Simulations for the spring and fall were run independently, because spring and fall populations are dependent on one another.

DISCUSSION

Model Evaluation

My model appeared to capture the behavior of bobwhite populations in the Rio Grande Plains. Simulated populations exhibited both boom-and-bust behavior typical of bobwhite populations in this ecoregion and possessed similar a population trajectory as that indicated by TPWD fall roadside counts. In addition, 5 of the 6 parameters compared between simulations and field observations were similar, and 6 of the

parameters were similar to values reported in the literature. My model therefore performed well and produced realistic estimates of bobwhite demographics in the Rio Grande Plains.

Density dependence.—An important finding of my model was the nature of the density-dependence relationship between spring population and fall population. Errington (1945) first described this relationship using a reverse logistic model and termed it the principle of inversity. I modeled density-dependent production using a linear relationship. Fitting a linear model to simulated data explained 15% of the variation in summer increase which was comparable to prior research (25.0%; Guthery et al. 2000*a*). Various models, including a linear model, have been used to describe the relationship between percent summer gain and spring breeding density (Roseberry and Klimstra 1984:Table 18). In these models, spring density explained 14.5–82.0% in percent summer gain. A logarithmic model explained only 10% of the variation in my simulated data. I expected a linear model to explain more of the variation in absolute summer gain given that density-dependent reproduction in the simulation model was described as a linear relationship. However, a logarithmic model explained 33.0% of the variation in the fall population supporting the possible existence of an asymptotic limit (i.e., carrying capacity or Guthery et al. (2000*a*) definition of demographic capacity). It is plausible that the true nature of the density-dependent relationship on my study area lies somewhere between a linear and logarithmic model. However, it appears that a linear model of density dependence adequately characterizes the relationship.

Sensitivity Analysis

Parameters relating directly to production (nesting attempts/hen, nest survival, and proportion of hens nesting, female sex ratio at hatch, and density-dependent reproduction) had the greatest influence on the modeled fall bobwhite population on my study area, which had an estimated $\lambda = 1.45$. My results follow those of Guthery et al. (2000*a*) largely because their and my models had $\lambda \geq 1$. Guthery et al. (2000*a*) found that survival, production, and demographic capacity were the most management–sensitive variables in there prototype bobwhite population. Sandercock et al. (2008) reported that winter, summer, and chick survival had the greatest contributions to the variance of rate of population change for declining bobwhite populations ($\lambda < 1$).

Population parameters having the greatest influence on that population's trend will depend on if the population is declining, stable, or increasing. For example, if a population is declining, then survival should be an important parameter because individuals in the population need to survival long enough to reproduce. However, if the population is stable or increasing, then production should be the most important parameter because survival can decrease, but there will still sufficient individuals in the population to reproduce maintain the population trend.

These results are intuitive from a life history standpoint. Bobwhites are a short lived species, have high mortality rates, and a high reproductive potential (Burger et al. 1995, Guthery 2000:119, Sandercock et al. 2008). Saether and Engen (2002) report that avian species with life history characteristics that include higher specific growth rates, large stochastic effects on the population dynamics, and strong density regulation at low

densities are found in species with large clutch sizes or high adult mortality rates, rather than in long-lived species. Bobwhites in south Texas would tend to fall into that category. They are a short-lived species, live in a very stochastic environment which effects production, exhibit density-dependent reproduction and mortality, and have large clutch sizes. Stahl and Oli (2006) found a general trend that that avian populations that matured early and had high reproductive rates were characterized by population growth rates most sensitive to changes in reproductive parameters and populations that matured late and had low reproductive rates had population growth rates most sensitive to survival parameters. It makes sense that parameters that have a large impact on production would have the largest impact on fall bobwhite populations in south Texas because of the species life history characteristics and the stochastic environment that it occupies.

Care must be taken when interpreting the sensitivity of λ to demographic parameters. Demographic parameters contain both sampling variation and process variation. For management to be successful it is important to understand the process variation in order to develop sound management strategies that produce a desired outcome. Other variables, such as cost of management actions, time scales, personnel, etc. also need to be considered when implementing management actions.

Population Persistence

Following the quasi–extinction criteria of $\leq$14 birds, the probability of persistence for 100 years for my simulated population was 91.7% for the fall and spring populations compared to 95% probability of Guthery et al. (2000*a*). The population modeled by

Guthery et al. (2000*a*) experienced both summer and winter catastrophes. A population experiencing summer catastrophes and a harvest rate of ≤30% would require a demographic capacity of 700 birds (Guthery et al. 2000*a*).

Because my model was based on an initial starting condition of 500 chicks, which resulted in a population persistence of 72.5% for the fall populations the nest logical question is how many adult bobwhites would be needed to produce 500 chicks? The winter age ratio from my study sites was 2.85 juveniles:adult. On average, this would require about 175 adults to produce 500 chicks. Guthery et al. (2000*a*) reported that about 100 birds were needed for 95% population persistence with summer catastrophes and no hunting. Hunting did occur on my study area, but hunting pressure was controlled by a lease manager who kept pressure at levels that would enhance the bobwhite population on the lease. Hunting pressure on the area probably never approximated 30%. Therefore, my demographic estimate of 175 birds seems reasonable for my study area. This would result in a spring (i.e., pre-breeding) density on my study area of 0.22 birds/ha which is tenable.

One possible reason that the demographic capacity reported by Guthery et al. (2000*a*) is lower than mine because of the low quasi-extinction criteria that they used. I increased the quasi-extinction criteria to a more conservative 40 birds (0.05 birds/ha), which resulted in a 74.2% probability of persistence (simulations had ≥1 year with ≤40 birds) for the spring population and a 72.5% probability of persistence for the fall population. Increasing the quasi-extinction criteria decreased the persistence probability by 19.1% for the spring population and 20.9% for the fall population. The lower the

quasi-extinction criteria in a stochastic model, the larger the population will need to be to evade extinction.

Even with any potential biases associated with attaching radio transmitters to bobwhites, my modeled population had a 74.2% probability of persistence for the spring population and a 72.5% probability of persistence for the fall population. Therefore, radio telemetry based estimates of bobwhite demography can yield reasonable results if proper protocols are followed (i.e., not radio-marking birds that weigh ≤150 g). It appears that production of about 500 chicks was sufficient for population persistence on my study area.

Population Dynamics

My model provided support for dynamics that were suspected to occur in bobwhite populations and new information about the distributions of some bobwhite demographic parameters. The 100-year projection of the mean annual fall population for each year of the 120 simulations (Fig. 3.6) varied symmetrically about the average mean fall population (1,031 birds). This resulted in an average fall density of 1.29 birds/ha on my study area.

Population parameters that influence production (nesting attempts/hen, nest survival, and proportion of hens nesting, female sex ratio at hatch, and density-dependent reproduction) had the greatest influence on the ending fall population. Production is important for maintaining south Texas bobwhite populations based on their life history characteristics (Guthery and Kuvlesky 1998), the stochastic environment that they occupy, and the sensitivity analysis that I conducted.

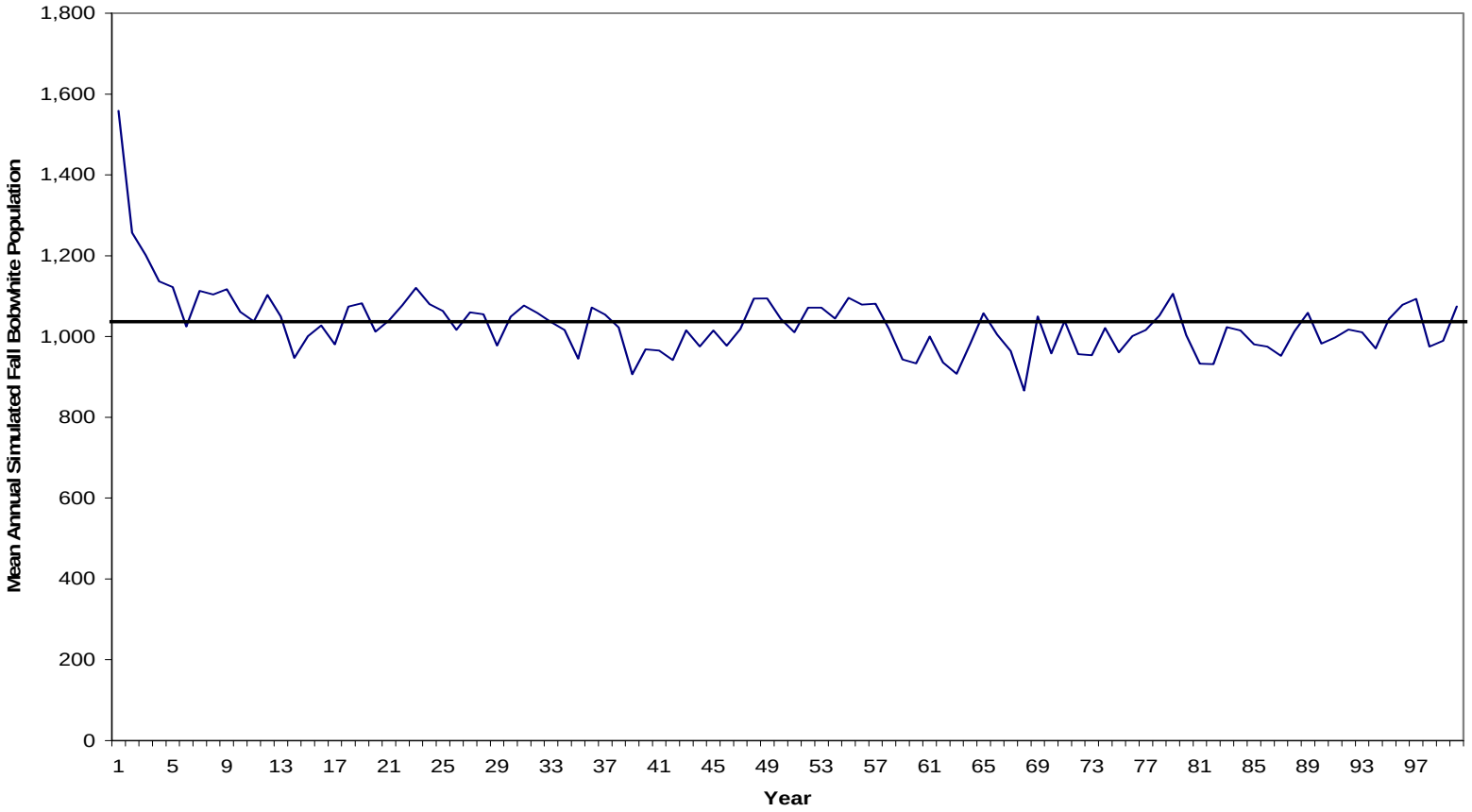

Figure 3.6. Mean annual fall bobwhite population trend for 100 years. Annual mean based on 120 simulations. Solid line represents the mean of the 100 year averages (1,031 individuals).

Annual survival rates.—My estimates of simulated annual survival varied by sex. Bobwhite survival is known to vary by sex (Pollock et al. 1989*a*, Palmer and Wellendorf 2007, Terhune et al. 2007) The greatest reported difference in annual survival rate between sexes has been 23.5% (Pollock et al. 1989*a*) and the smallest 14.9% (Terhune et al. 2007). DeMaso et al. (1998) reported that monthly mortality rates, the complement to survival, differed by ≥43.5% between bobwhite sex and age classes in western Oklahoma.

Simulated annual survival for adult males is comparable to other estimates reported in the literature, which are questionable because of demographic performance and persistence of the population (Guthery and Lusk 2004). Based on observed winter age ratios from my study area and the theoretical relationship between annual survival and age ratios, (Guthery 1997), annual survival for the population assuming stability would be about 0.27. If $\lambda = 1$, and survival and recruitment are stable from N_t to N_{t+1} then $S = 1/(1 + R)$ where S = annual survival rate and R = age ratio. The theoretical relationship lacks empirical evidence. Guthery (1997) assumed that years with low annual survival would have to have high production. I made no such assumptions in my model, both survival and production parameters were randomly drawn from their distributions, yet resulted in winter age ratios that have been reported for south Texas (Lehmann 1984:133). This suggests that the theoretical relationship proposed by Guthery (1997) between bobwhite annual survival and winter age ratios does not hold for non-stable populations.

Lastly, there appears high variability in bobwhite annual survival within study sites (Guthery and Lusk 2004:Table 1; Palmer and Wellendorf 2005:Table 3; Terhune et al. 2005:Table 3). The distribution of simulated female, adult annual survival (Fig. 3.7) and simulated male, adult annual survival (Fig. 3.8) are skewed, which indicates high variability. Long-term studies, with adequate sample sizes in age and sex classes will be required to obtain more accurate and precise annual survival estimates, more information about the distribution of the those estimates, and a better understand the variability associated with bobwhite survival.

Spring and fall density.—My observed spring densities are higher than my observed fall densities. This is because spring observed estimates are based on a small sample size ($n = 2$). Also, if immigration was occurring on my study area, that might explain the higher spring densities. The distributions of simulated fall (Fig. 3.9) and spring densities (Fig. 3.10) are what is observed in the field, with fall densities skewed right (i.e., higher densities) and spring densities shifted left (i.e., lower densities). Both fall (Fig. 3.9) and spring (Fig. 3.10) distributions are have long left tails, indicating high variability in these parameters.

Finite rate of increase (λ) in the fall population.—My observed and simulated λ are consistent with λ estimates for bobwhite populations published in the literature (Table 2). Doubling of the fall population occurs, but is a rare event in bobwhite populations. A $\lambda \geq 2.0$ did not occur in any of Rosene's (1969:Appendix G) or Roseberry and Klimstra's (1984:73) data. Using data with a time series >10 years, Errington's (1945) fall population doubled 14.3% of the time (2 of 14 years) and

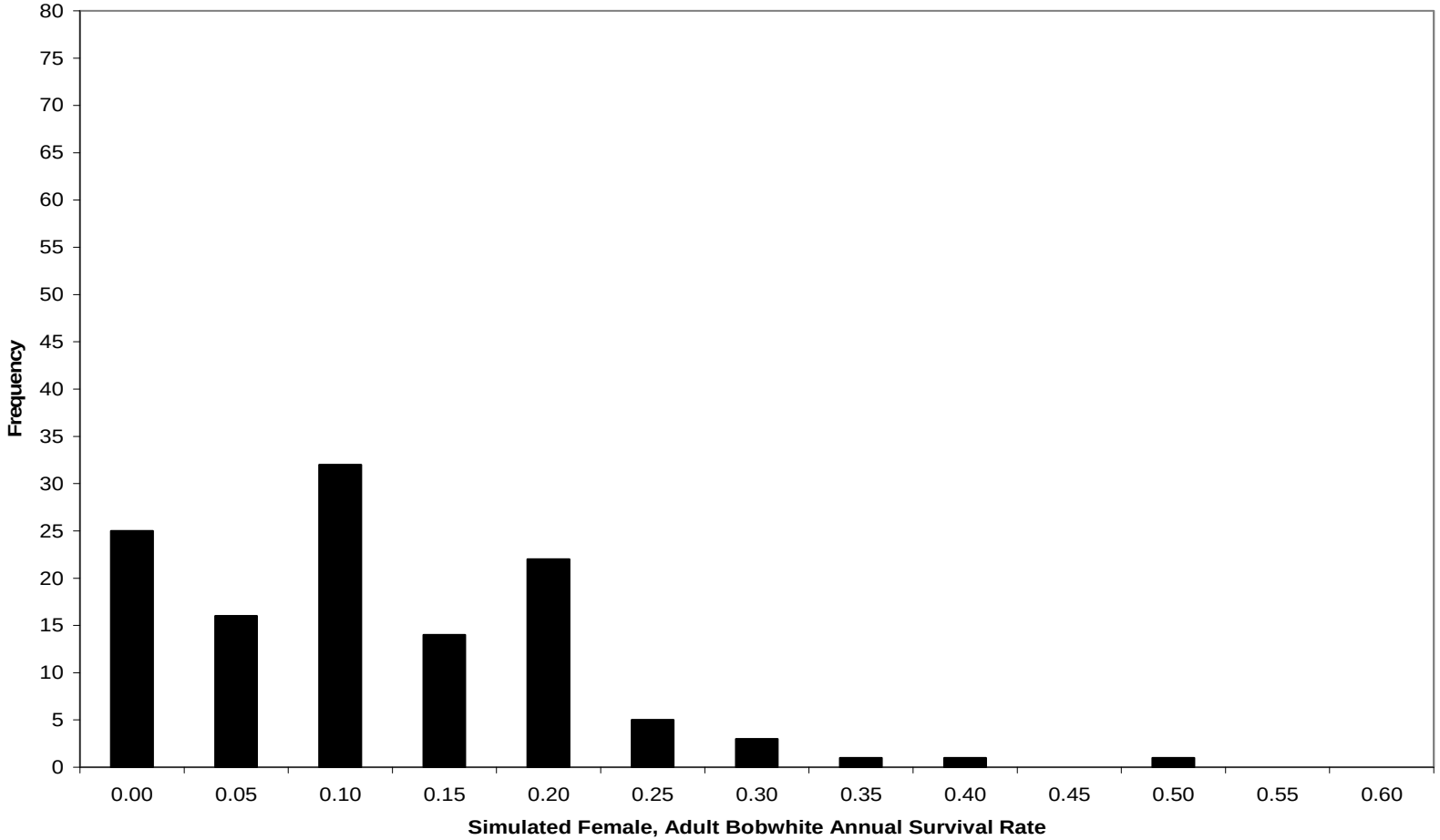

Figure 3.7. Distribution of simulated female, adult bobwhite annual survival rate (n = 120 simulations).

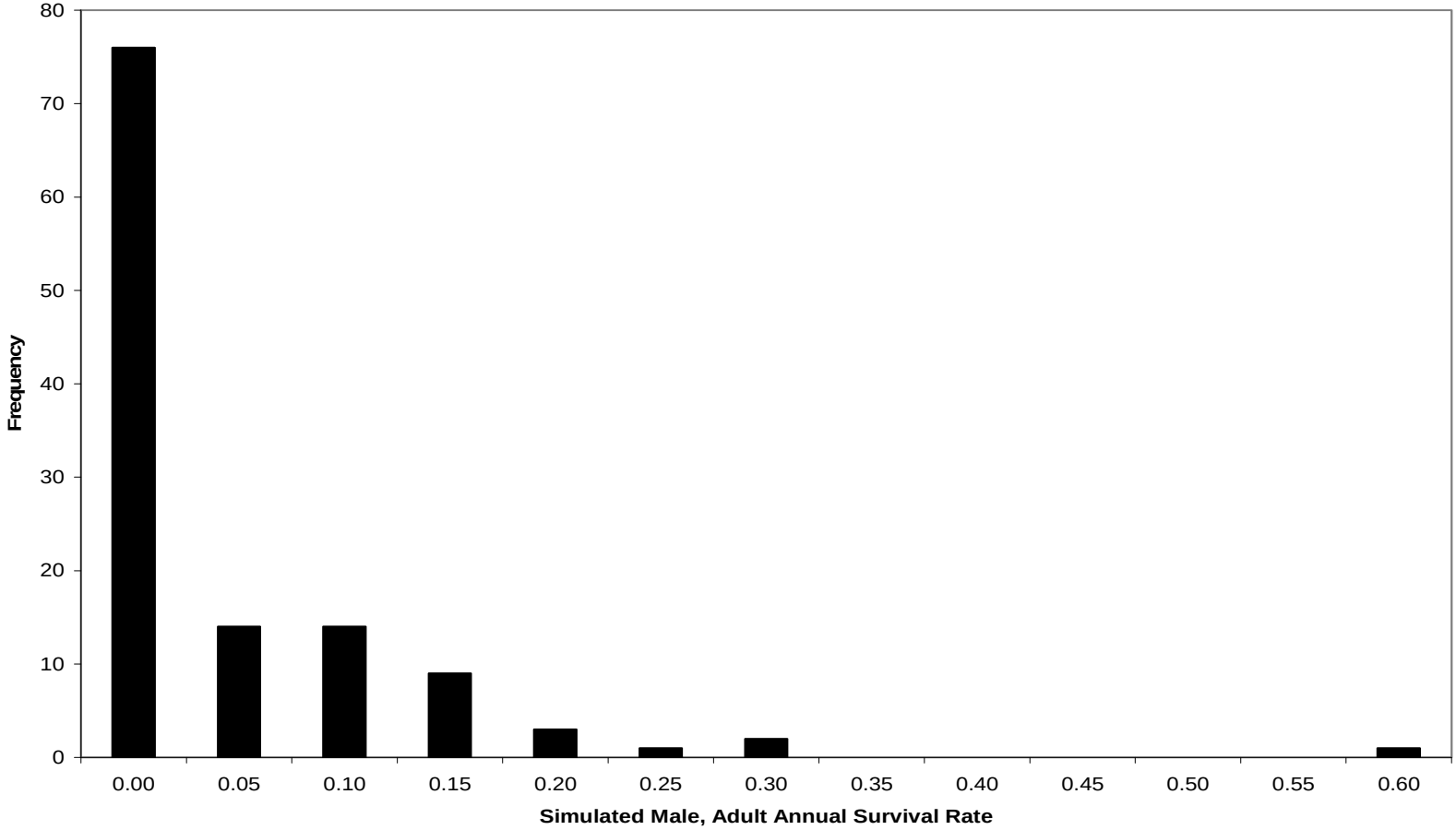

Figure 3.8. Distribution of simulated male, adult bobwhite annual survival rate (n = 120 simulations).

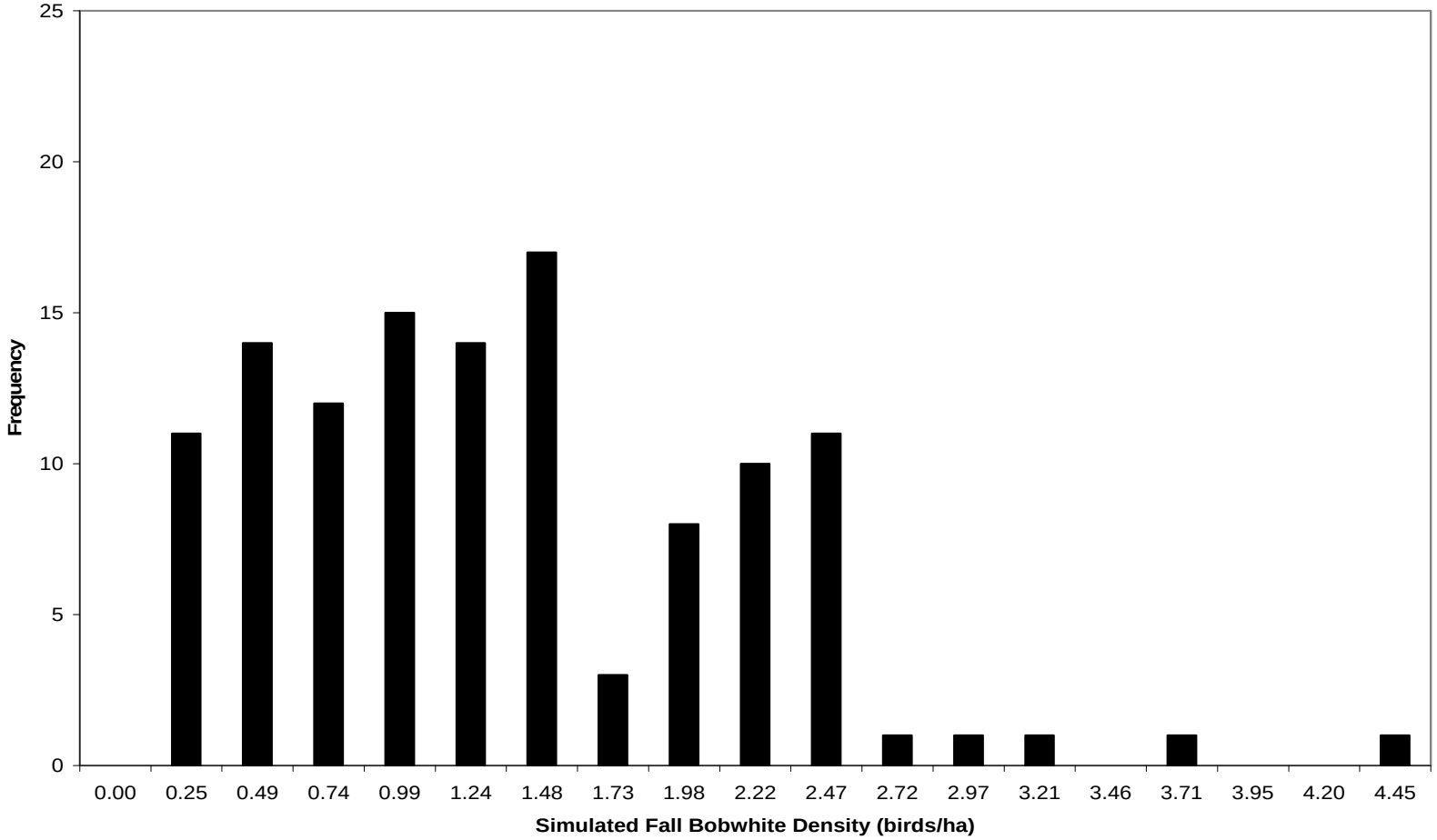

Figure 3.9. Distribution of simulated bobwhite fall density (birds/ha) (n = 120 simulations).

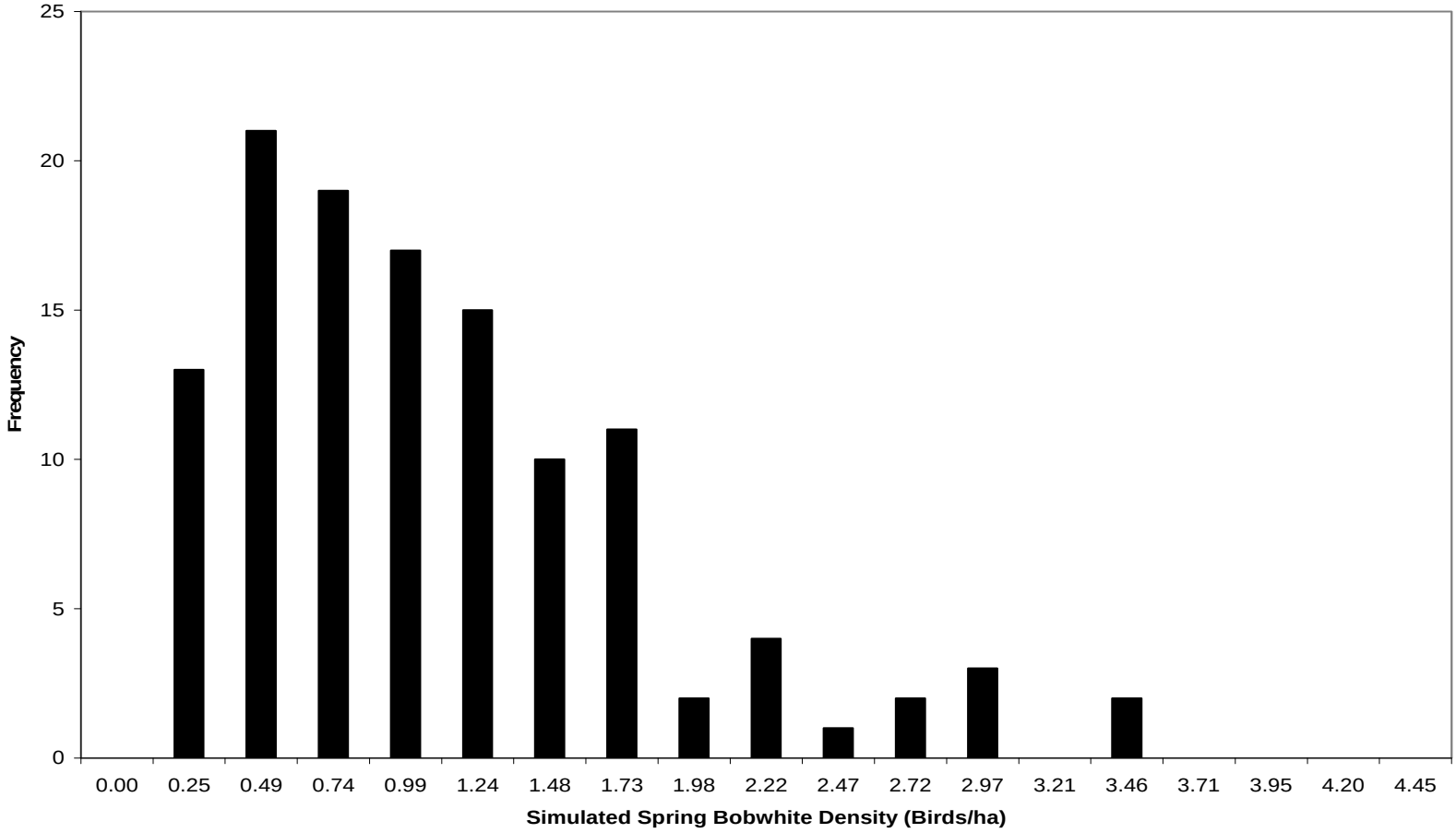

Figure 3.10. Distribution of simulated bobwhite spring density (birds/ha) (n = 120 simulations).

TPWD's (TPWD 2008) data for August roadside counts doubled 10.4% of the time (3 of 29 years). Doubling of the fall population occurred 20.8% (25 of 120 simulations) of the time in my simulated population (Fig. 3.11). The distribution of λ is skewed left with a long tail indicating high variability with this demographic parameter (Fig. 3.11).

Winter age ratios.—My simulated winter age ratios were similar to those reported for Texas (Table 2). Only 12 of 120 (10.0%) simulations yielded biologically unreasonable (>7 juveniles:adult) (Fig. 3.12) winter age ratios. The distribution of winter age ratios is skewed left with a long tail indicating high variability with this parameter (Fig. 3.12).

Most of the demographic parameters from my simulation model provided realistic, similar estimates to what was observed on my study area and what is reported in the bobwhite literature. I challenged my model with various independent data (density estimates, winter age ratios, and λ from TPWD survey data) and my model results were similar to estimates from the independent data. This strengthens that support that our model performs well for bobwhite populations in southern Texas.

MANAGEMENT IMPLICATIONS

Modeling allows the identification of gaps in knowledge (Guthery et al. 2000*a*). My model appears to be a good predictor of bobwhite populations in the Rio Grande Plains. However, I feel that my model could be improved by better understanding of density dependent effects on bobwhite populations, better estimates of immigration and emigration, and more precise estimates of various age and sex classes of bobwhites in the Rio Grande Plains. Also, estimates of juvenile survival are needed, especially from

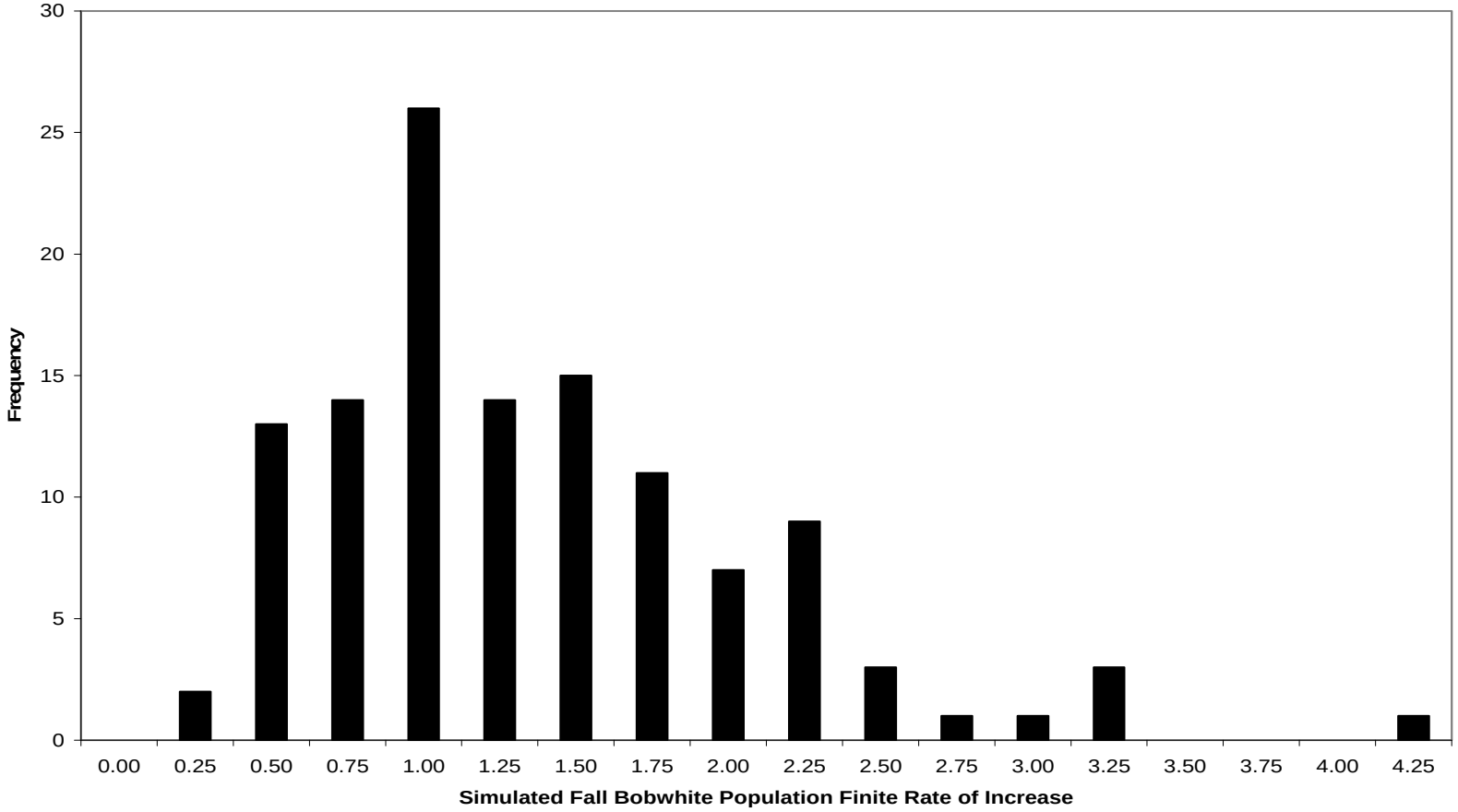

Figure 3.11. Distribution of simulated fall bobwhite population finite rate of increase (n = 120 simulations).

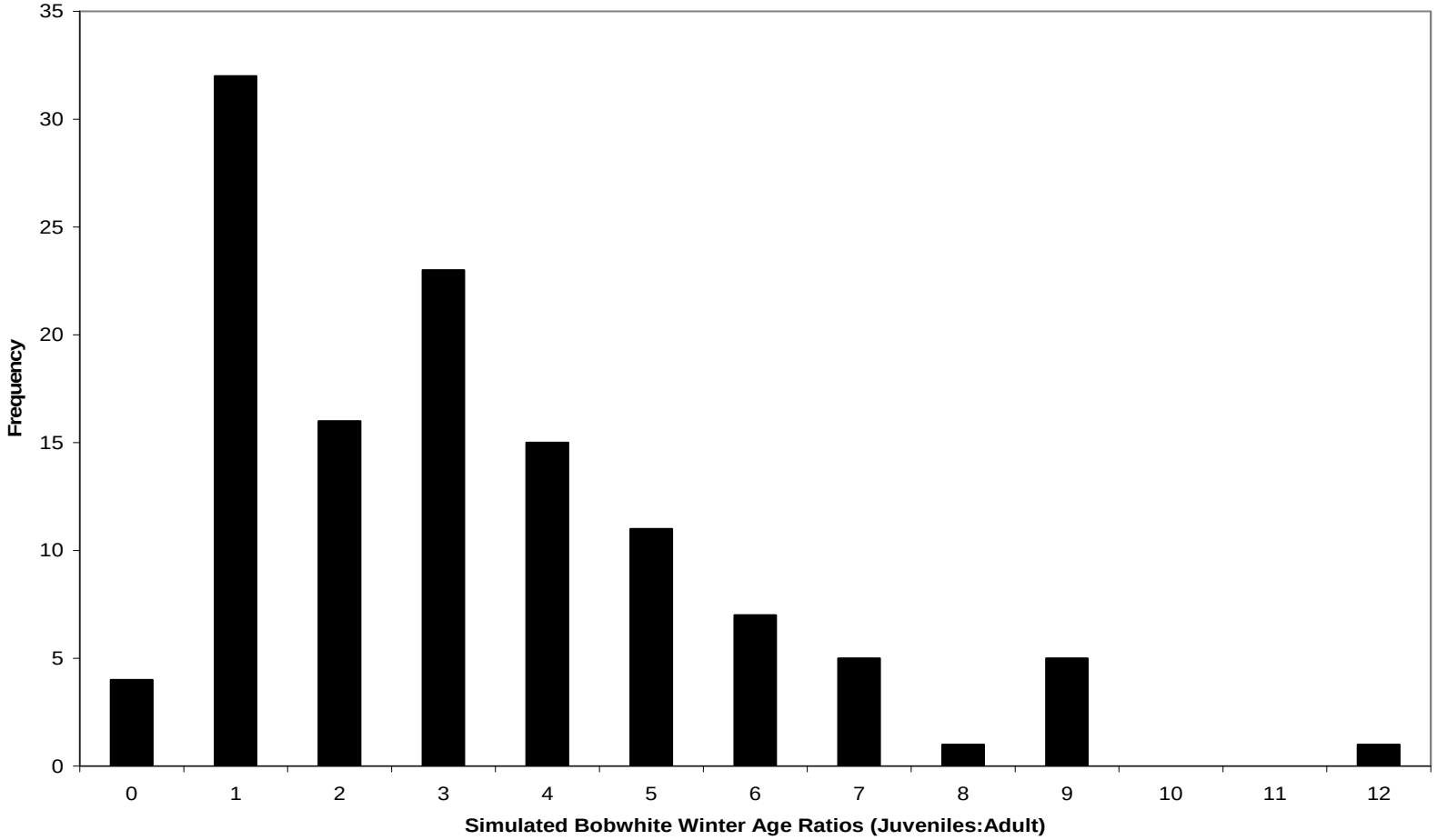

Figure 3.12. Distribution of simulated bobwhite winter age ratios (juveniles:adult) (n = 120 simulations).

hatching to an age of about 150 days, when survival can be estimated via radio telemetry. The addition of other simulation sub models, such as weather, habitat, management, and harvest to my population model could allow mangers to see their management actions impact bobwhite populations before they are actually implemented. Below I use my model to investigate the quality of bobwhite hunting and the frequency of that quality on my study area.

Guthery (1986:147–148) reported south Texas bobwhites at low densities, 0.6 birds/ha resulted in about 0.5 coveys/hour being encountered by randomly walking and high densities, 2.5 birds/ha resulted in about 2.0 coveys/hour. Palmer et al. (2002) found a high correlation ($r^2 = 0.77$) between coveys moved per hour and bobwhite density in southwest Georgia. Palmer et al. (2002) show that low densities, 0.7 birds/ha resulted in 0.5 coveys/hour, with systematic hunting at high densities, 3.0 birds/ha resulted in 2.9 coveys/hour of hunting.

Based on the densities reported by Guthery (1986:147–148) and Palmer et al. (2002) extrapolated to my study area (800 ha), excellent bobwhite hunting would be expected with a fall population ≥1,752 birds, average hunting with >500 and <1,752, and poor hunting with ≤500 birds. Based of the distribution of simulations of the fall bobwhite population (Fig. 3.13) hunters and managers can expect poor hunting seasons to occur 25.0% of the time (30 of 120 simulations), average hunting conditions to occur 54.2% of the time (65 of 120 simulations, and excellent hunting conditions to occur 20.8% of the time (25 of 120 simulations). The distribution of the simulated spring population (i.e., spring density, Fig. 3.10) is shifted left of the fall population (i.e., fall

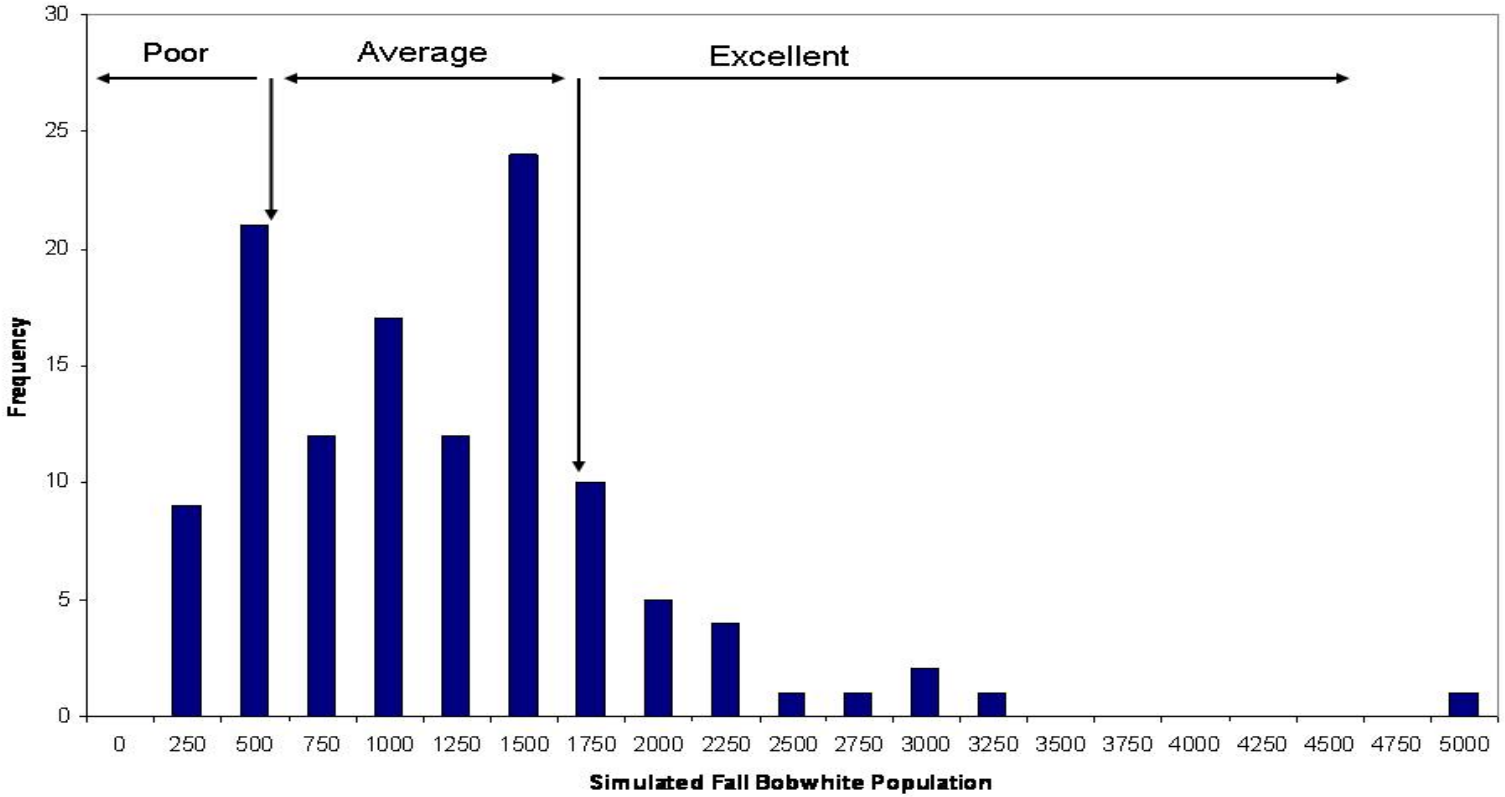

Figure 3.13. Distribution of simulated fall bobwhite population (n = 120 simulations). Poor hunting ≤500 birds, average hunting >500 birds, but <1,750 birds, and excellent hunting ≥1,750 birds.

density, Fig. 3.9), because spring bobwhite populations are usually lower than the fall populations, unless immigration is occurring.

CHAPTER IV

HABITAT INFLUENCE ON DEMOGRAPHIC PERFORMANCE: EFFECT OF BRUSH COVER ON NORTHERN BOBWHITE ABUNDANCE, PRODUCTIVITY, AND SURVIVAL IN SOUTHERN TEXAS

Previous research has been devoted to quantifying the habitat needs and selection for many wildlife species. However, how habitat use affects the long-term demographic performance of a species has been ignored. Woody vegetation is an important component of northern bobwhite habitat. Bobwhites use woody vegetation for food (Jackson 1969, Guthery 1986:16, Lehmann 1984:187), thermal cover (Forrester et al. 1998, Hiller and Guthery 2005), loafing cover (Guthery 1986:4–7, Johnson and Guthery 1988), and escape cover from predators (Jackson 1969, Guthery 1986:7, Kopp et al. 1998).

The amount of BCC needed by bobwhites has been previously documented by various researchers (Schroeder 1985, Johnson and Guthery 1988, Bidwell et al. 1991, Rice et al. 1993, Kopp et al. 1998, Guthery et al. *2000b*). However, recommendations for the amount of woody cover has varied greatly ranging from a low of ~5% (Guthery 1986:18, 115) to a high of 85% (Guthery et al. 2000*b*:Fig. 2). Kopp et al. (1998) reported that bobwhites avoided patches with <20% BCC and preferred patches with 20–60% BCC at flushing and landing points. The wide range of BCC values has made BCC management for bobwhites somewhat of a contentious issue.

Most of the above estimates are based on the presence (Forrester et al. 1998, Kopp et al. 1998) or density (Rice et al. 1993) of bobwhites. However, how habitat selection affects bobwhite population parameters has been ignored. Production and survival (i.e., fitness) in bobwhite populations are important parameters leading to increases and viability in those populations (Guthery et al. 2000*a*, Sandercock et al. 2008). Therefore, a study that examines the effect of quality and/or quantity of habitat on bobwhite abundance, productivity, and survival is warranted.

My objective was to compare bobwhite density (spring and fall density), productivity, and survival among 3 study sites with varying amounts of BCC. I also compared demographic performance of bobwhite populations in these different cover classes using a simulation model (Chapter III) to test the hypothesis that BCC had a long-term (i.e., 100 years) impact on bobwhite populations.

STUDY AREA

The study area is located on a private hunting lease on the Encino Division of King Ranch, Brooks County, Texas which lies within the Rio Grande Plains ecoregion (Gould 1975). The study area consisted of 3 spatially-independent experimental units (i.e., pastures): North Viboras (1,966 ha), La Loba (1,379 ha), and Cuates (1,240 ha). Experimental units were arranged north to south, respectively, and were separated by ~5 km from each other. A woody cover gradient occurred from north to south, with woody cover decreasing on a southerly gradient. Woody canopy cover was >30% (North Viboras), ~25% (La Loba), and ~10% (Cuates) (Rusk 2006).

Vegetation in the Rio Grande Plains ecoregion is characterized as a mixed-brush community (Scifres 1980:30). Vegetation specific to the study area consisted predominantly of honey mesquite (*Prosopis glandulosa*), huisache (*Acacia smallii*), granjeno (*Celtis pallida*), live oak (*Quercus virginiana*), and pricklypear cactus (*Optuntia lindheimeri*) (Hernández et al. 2002). Predominant forbs included croton (*Croton* spp.), sunflower (*Helianthus annuus*), dayflower (*Commelina erecta*), and partridge pea (*Chamaecrista fasciculata*) (Hernández et al. 2002). Common grasses included little bluestem (*Schizachyrium scoparium*), paspalum (*Paspalum* spp.), three awn (*Aristida* spp.), gulf cordgrass (*Spartina spartinae*), King Ranch bluestem (*Bothriochloa ischaemum*), Kleberg bluestem (*Dichanthium annulatum*), sandbur (*Cenchrus incertus*), red lovegrass (*Eragrostis secundiflora*), and buffelgrass (*Pennisetum ciliare*) (Hernández et al. 2002).

Climatic conditions are classified as semi-arid, sub-humid and are characterized by a high rate of evaporation (Williamson 1983). The months of June and September receive the greatest amount of precipitation. Monthly precipitation ranges from 1.4–13.0 cm with a mean annual rainfall of 65.4 cm (Williamson 1983). The 33-year mean temperature is 22.3 C (range 13.1–29.8 C). January is the coldest month ($\bar{x}$ = 13.1 C), and July is the hottest month ($\bar{x}$ = 29.8 C) (Williamson 1983).

METHODS

Field Data

Density.—Rusk et al. (2007) evaluated survey methods for estimating bobwhite density on my study area using distance sampling (Buckland et al. 2001). Transects

were developed in ArcMap and uploaded onto field computers so survey effort and detections could be monitored in the field to determine if the necessary sample size (i.e., >60 detections) and effort (i.e., 91-km of effort) was accrued. The number and length of transects varied per pasture because of the shape of the pasture perimeter. Transects were traversed during the first and/or last 3 hours of daylight. Transects were flown at a height of 7 m and a velocity of 37 km/hour using a Robinson R44 (Robinson Helicopter Company, Torrance, California). Pilots utilized an Envizio plus lightbar (Raven Industries, Sioux Falls, South Dakota) to navigate transects. The recorded perpendicular distances were analyzed with Program DISTANCE 5.0 (Thomas et al. 2004). The best detection function was chosen based on Akaike's Informatin Criterion (AIC) values and goodness of fit using Chi-square analysis (Buckland et al. 2001). Surveys were conducted by randomly selecting the starting transect and flying the subsequent transect that was 400-m away. I continued with this scheme in a sequential manner until all transects were traversed. I used density estimates derived from helicopter transects for fall (Oct–Dec 2005–2007) and spring (Mar 2007–2008) (Rusk et al. 2007, M. J. Schnupp, Caesar Kleberg Wildlife Research Institute, unpublished data) to evaluate the performance of my simulation model.

Productivity.—I captured bobwhites using standard funnel traps (Stoddard 1931:442) and night-netting (Labisky 1968) throughout the study (2000–2005). Individuals were classified by sex and age (Rosene 1969:44–54), leg-banded, and birds weighing over 150 g were fitted with a 5–6 g neck-loop radio transmitter (Shields et al. 1982) (American Wildlife Enterprises, Tallahassee, Florida, USA). Radio-marked

bobwhites were located >2 weekly and >3/week during the nesting season (Apr–Oct). Bobwhites were monitored throughout the year, which was partitioned into 4 seasons based on bobwhite life history: breeding (spring; 1 Mar–31 May), nesting (summer; 1 Jun–31 Aug), covey pre-frost (fall; 1 Sep–30 Nov), and covey post-frost (winter; 1 Dec–28 Feb).

I used radio-marked bobwhites to estimate the proportion of hens that entered the nesting season (15 Apr) and attempted to nest, regardless of the nest fate and regardless if the hen survived the nesting season. This sample therefore included hens that entered the nesting season but died before having a nesting opportunity or before a nest could be found. I also used these hens to determine the number of nesting attempts per hen. I assumed nesting when I obtained consecutive locations of a radio-marked bird at the same point and located nests by homing. When a nest was found, I continued monitoring until nesting was terminated (i.e., abandoned, depredated, or hatched). Once a nest was terminated, I estimated the clutch size. I also determined the frequency of nests that hatched during season 2 and 3 regardless of nest fate.

I defined productivity (*Prod*) as the number of chicks produced during the spring and/or the summer nesting season. Productivity was calculated deterministically as

$$Prod = Breed * Clutch * NestSurv * NestAttempt * PropNest,$$

where *Breed* is the number of adult females entering the spring breeding season, *Clutch* is the clutch size, *NestSurv* is the estimate of daily nest survival (0.9593) from Radar et al. (2007), raised to the 23 power to estimate nest survival for the 23-day incubation period, *NestAttempt* is the number of nesting attempts per adult female that enter the

nesting season and nest during that nesting season (spring and summer, regardless of whether they survived the nesting season), and *PropNest* is the proportion of adult female bobwhites that enter the nesting season and nest during the spring and/or the summer nesting seasons, regardless of whether they survive the nesting season.

Survival.— Survival rates were calculated using the Kaplan-Meier estimator (Kaplan and Meier 1958) and staggered-entry approach (Pollock et al. 1989*b*, Pollock 1989*c*) to estimate seasonal survival. I assumed that birds were randomly sampled, survival times for individuals were independent, left-censored individuals (staggered entry) had survival distributions similar to previously marked individuals, and causes for censoring (i.e., radio failure) were independent of the birds fate. I only included bobwhites surviving >14 days after radio-marking to minimize trapping or handling bias on survival probabilities (Pollock et al. 1989*b*, Pollock et al. 1989*c*, White and Garrott 1990).

Simulation Model

The model is described in detail in Chapter III. Briefly, the model represented production and survival of adult and juvenile, female and male radio-marked bobwhites on an 800-ha study area in the Rio Grande Plains. Chicks produced during seasons 2 and 3 were separated into female and male juvenile segments of the population. Seasonal mortality was removed from each segment of the population (female juvenile, female adult, male juvenile, male adult). The juvenile cohorts entered the adult cohort in season 1 and remain there throughout their lifetime. Egress and ingress were assumed to be equal (Guthery 2002:45).

I included density-dependent mortality (Roseberry and Klimstra 1984:54) and density-dependent production (Errington 1945, Cookingham and Ripley 1964, Roseberry and Klimstra 1984:96) in my model. Data collected via radio telemetry during 2000–2005 were used to estimate demographic parameters and their Weibull distributions (See the Variable Distributions to Invoke Stochasticity section in Chapter III). Variables were randomly drawn from these distributions to give the model stochasticity.

The model was developed using STELLA® 9.0.2 software (ISEE Systems, Incorporated, Lebanon, New Hampshire, USA). It was based on difference equations where Δt = 3 months with stochastic variables randomly drawn from their Weibull distributions. I ran simulations for 100 years and evaluated model output for biological reasonable results.

Statistical Analysis

I compared demographic parameters among BCC classes using 95% confidence intervals for univariate comparisons (Johnson 1999). I also compared a deterministic estimation of chick production assuming a breeding population of 100 birds, constant nest survival rate of 0.3845 (Rader et al. 2007), and using the pooled values of the deompgraphic variables. I evaluated the long-term influence of habitat on demographic performance by estimating the probability of population persistence using a quasi–extinction criteria of <0.05 bobwhites/ha (≤40 bobwhites for my study area). This criterion was based on minimum spring densities reported in the literature (Spears 1991).

This criterion is below the 0.25 bobwhites/ha considered to be indicative of very poor bobwhite populations (Guthery 1986:149)

RESULTS

Univariate Comparisons

All demographic parameters were similar among the 3 BCC classes. These included fall and spring densities (Table 4.1), the mean proportion of females alive and entering the nesting season (Table 4.2), clutch size (Table 4.3); the mean proportion of females attempting to nest (Table 4.4), the mean number of nesting attempts/female (Table 4.4), and empirical estimates of seasonal survival (Table 4.5). The deterministic estimation of chick production resulted in the production of 309, 241, and 314 chicks for the ~10%, ~25%, and >30% BCC classes, respectively. Brush canopy cover therefore did not appear to influence short-term demographic performance.

Long-term Demographic Performance

Simulation modeling indicated that chick production, fall density, fall population, and spring population were lower on the ~10% BCC treatment than on the other 2 treatments, which were similar (Table 4.6). The fall population (Fig. 4.1) and spring population (Fig. 4.2) long-term trend for the ~10% BCC treatment was lower than the other 2 treatments. Simulated winter age ratios were higher on the >30% BCC treatment and lower, but similar on the other 2 treatments (Table 4.6). The probability of fall population persistence was greater in the ~25% (90.8%) and >30% (100.0%) BCC

Table 4.1. Sample size (n), northern bobwhite density ($\hat{D}$; birds/ha), and standard error (SE) estimated using helicopter surveys with distance sampling methodology during fall (Oct–Dec) and spring (Mar) by brush canopy coverage class, during 2005–2008, Brooks County, Texas, USA.

Year	Brush canopy coverage								
	~10%			~25%			>30%		
Season	n	$\hat{D}$	SE	n	$\hat{D}$	SE	n	$\hat{D}$	SE
2005									
Fall	40	2.44	0.54	36	2.19	0.49	30	1.75	0.55
Spring[a]									
2006									
Fall	16	0.67	0.31	9	0.42	0.29	14	0.51	0.35
Spring[a]									
2007									
Fall	60	1.01	0.18	112	1.86	0.28	30	1.31	0.50
Spring	21	1.95	0.55	33	3.40	0.68	21	2.05	0.88

Table 4.1. Continued.

Year	Brush canopy coverage								
	~10%			~25%			>30%		
Season	*n*	$\hat{D}$	SE	*n*	$\hat{D}$	SE	*n*	$\hat{D}$	SE
2008									
Fall[b]									
Spring	9	0.19	0.13	26	0.75	0.28	21	1.23	0.45

[a]Spring surveys not conducted in 2005 or 2006.

[b]Fall surveys not completed at time of publication.

Table 4.2. The number and proportion of northern bobwhites that entered the nesting season (15 April), by brush canopy coverage class, sex, and year, 2001–2005, Brooks County, Texas, USA.

	Brush canopy coverage											
	~10%				~25%				>30%			
			Proportion				Proportion				Proportion	
Year	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
2001	16	10	0.62	0.38	17	8	0.68	0.32	10	7	0.59	0.41
2002	20	8	0.71	0.29	2	8	0.20	0.80	4	5	0.44	0.56
2003	40	11	0.78	0.22	12	9	0.57	0.43	11	5	0.69	0.31
2004	12	9	0.57	0.43	16	7	0.70	0.30	25	10	0.71	0.29
2005	13	10	0.57	0.43	7	6	0.54	0.46	11	8	0.58	0.42
Pooled	101	48	0.68	0.32	54	38	0.59	0.41	61	35	0.64	0.36

Table 4.3. Sample size (n), mean northern bobwhite clutch size ($\bar{x}$), and standard error (SE) by brush canopy coverage class and year, 2001–2005, Brooks County, Texas, USA.

	Brush canopy coverage														
	~10%					~25%					>30%				
Year	n	$\bar{x}$	SE	Min	Max	n	$\bar{x}$	SE	Min	Max	n	$\bar{x}$	SE	Min	Max
2001	14	12.4	0.6	9	17	18	11.5	1.0	1	19	12	12.9	1.0	8	19
2002	12	13.0	0.6	10	16	6	11.0	0.9	8	14	6	10.8	0.8	7	13
2003	24	12.3	0.5	8	19	16	11.3	0.5	8	16	23	12.4	0.5	9	18
2004	22	12.4	0.7	5	20	16	11.9	0.4	9	15	17	11.2	1.0	1	22
2005	12	11.4	0.6	9	16	9	11.7	0.7	9	16	15	11.1	0.5	9	17
Pooled	84	12.3	0.3	5	20	65	11.5	0.3	1	19	73	11.8	0.4	1	22

Table 4.4. The proportion of female northern bobwhites that entered the nesting season on 15 April that attempted to nest, the proportion that didn't attempt to nest, and the number of nesting attempts per hen regardless if they survived the nesting season by brush canopy coverage class and year, 2001–2005, Brooks County, Texas, USA.

	Brush canopy coverage								
	~10%			~25%			>30%		
Year	Nesting	Not nesting[a]	Nests/hen	Nesting	Not nesting[a]	Nests/hen	Nesting	Not nesting[a]	Nests/hen
2001	0.54	0.46	1.4	0.71	0.29	1.3	0.63	0.37	1.4
2002	0.77	0.23	1.7	1.00	0.00	2.0	0.50	0.50	3.0
2003	0.56	0.44	1.9	0.60	0.40	1.3	0.80	0.20	2.5
2004	0.75	0.25	1.7	0.77	0.23	1.3	0.56	0.44	2.0
2005	0.50	0.50	1.2	0.71	0.29	1.0	0.44	0.56	1.5
Pooled	0.60	0.40	1.6	0.71	0.29	1.3	0.57	0.43	1.9

[a]Includes hens that entered the nesting season on 15 Apr, but may have died before they attempted to nest.

Table 4.5. Sample sizes[a] (n), empirical estimates of mean northern bobwhite seasonal survival ($\hat{s}$), and standard error (SE) by brush canopy coverage treatment for spring (1 Mar–31 May), summer (1 Jun–31 Aug), fall (1 Sep–30 Nov), and winter (1 Dec–28 Feb) by age and sex during 2001—2005, Brooks County, Texas, USA. Tabulated means represent empirical analysis of the Kaplan–Meier survival estimates.

	Brush canopy coverage														
Sex															
Age	~10%					~25%					>30%				
Season	n	$\hat{s}$	SE	Min	Max	n	$\hat{s}$	SE	Min	Max	n	$\hat{s}$	SE	Min	Max
Female															
Adult															
Spring	5	0.506	0.072	0.357	1.000	5	0.654	0.106	0.360	1.000	5	0.472	0.100	0.200	0.706
Summer	5	0.512	0.051	0.356	0.667	5	0.723	0.029	0.661	0.800	5	0.600	0.132	0.292	1.000
Fall	5	0.744	0.103	0.484	1.000	5	0.666	0.100	0.432	1.000	5	0.751	0.053	0.550	0.856
Winter	5	0.622	0.116	0.267	1.000	5	0.784	0.103	0.540	1.000	5	0.618	0.159	0.250	1.000
Juvenile															

Table 4.5. Continued.

	Brush canopy coverage														
Sex															
Age	~10%					~25%					>30%				
Season	*n*	$\hat{s}$	SE	Min	Max	*n*	$\hat{s}$	SE	Min	Max	*n*	$\hat{s}$	SE	Min	Max
Spring	1	0.625		0.625	0.625										
Summer	1	0.750		0.750	0.750	1	0.818		0.818	0.818	1	0.167		0.167	0.167
Fall	1	1.000		1.000	1.000	2	0.917		0.833	1.000	1	1.000		1.000	1.000
Winter	4	0.833	0.096	0.667	1.000	4	0.249	0.111	0.000	0.539	4	0.856	0.144	0.424	1.000
Male															
Adult															
Spring	5	0.680	0.084	0.504	1.000	5	0.611	0.071	0.430	0.851	5	0.557	0.090	0.305	0.758
Summer	5	0.660	0.045	0.548	0.786	5	0.597	0.048	0.473	0.727	5	0.501	0.099	0.200	0.818
Fall	5	0.798	0.034	0.714	0.900	5	0.838	0.062	0.635	1.000	5	0.802	0.071	0.571	1.000
Winter	4	0.659	0.122	0.468	1.000	5	0.515	0.107	0.148	0.800	5	0.465	0.144	0.000	0.875

Table 4.5. Continued.

Sex / Age / Season	Brush canopy coverage														
	~10%					~25%					>30%				
	n	$\hat{s}$	SE	Min	Max	*n*	$\hat{s}$	SE	Min	Max	*n*	$\hat{s}$	SE	Min	Max
Juvenile															
Spring	1	0.500		0.500	0.500						1	0.595		0.595	0.595
Summer	1	0.714		0.714	0.714	2	0.357		0.000	0.714	2	0.714	0.286	0.429	1.000
Fall	2	0.900	0.100	0.800	1.000	2	0.360	0.100	0.800	1.000	3	1.000	0.000	1.000	1.000
Winter	3	0.488	0.244	0.000	0.750	3	0.293	0.244	0.714	0.750	4	0.688	0.138	0.333	1.000

[a]The number of seasonal estimates for that age and sex class, not the number of individual radio-marked bobwhites individual seasonal estimates were based on.

Table 4.6. Number of replicate simulations (*n*), mean ($\bar{x}$) northern bobwhite chick production, fall density (birds/ha), fall population, spring population, winter age ratio (juveniles:adult), and associated standard error (SE) by brush canopy coverage class, from northern bobwhite population simulation model, Brooks County, Texas, USA.

		Brush canopy coverage											
		~10%				~25%				>30%			
Parameter	*n*	$\bar{x}$	SE	Min	Max	$\bar{x}$	SE	Min	Max	$\bar{x}$	SE	Min	Max
Chicks produced	120	517.3	34.0	0.0	2,001.2	1,051.6	63.6	0.0	3,875.5	1,071.1	58.6	3.2	3,202.0
Fall density	120	0.8	0.05	0.0	1.2	1.8	0.08	0.1	4.8	1.8	0.08	0.4	4.4
Fall population	120	665.6	43.5	0.1	2,471.3	1,417.1	72.5	27.9	3,956.1	1,439.2	58.2	252.7	4,311.1
Spring population	120	600.7	36.9	6.6	2,194.4	1,261.8	53.7	166.7	3,417.7	1,239.6	53.5	268.5	2,986.9
Winter age ratio	120	2.6	0.16	0.0	9.4	2.4	0.18	0.0	13.7	3.8	0.30	0.0	16.5

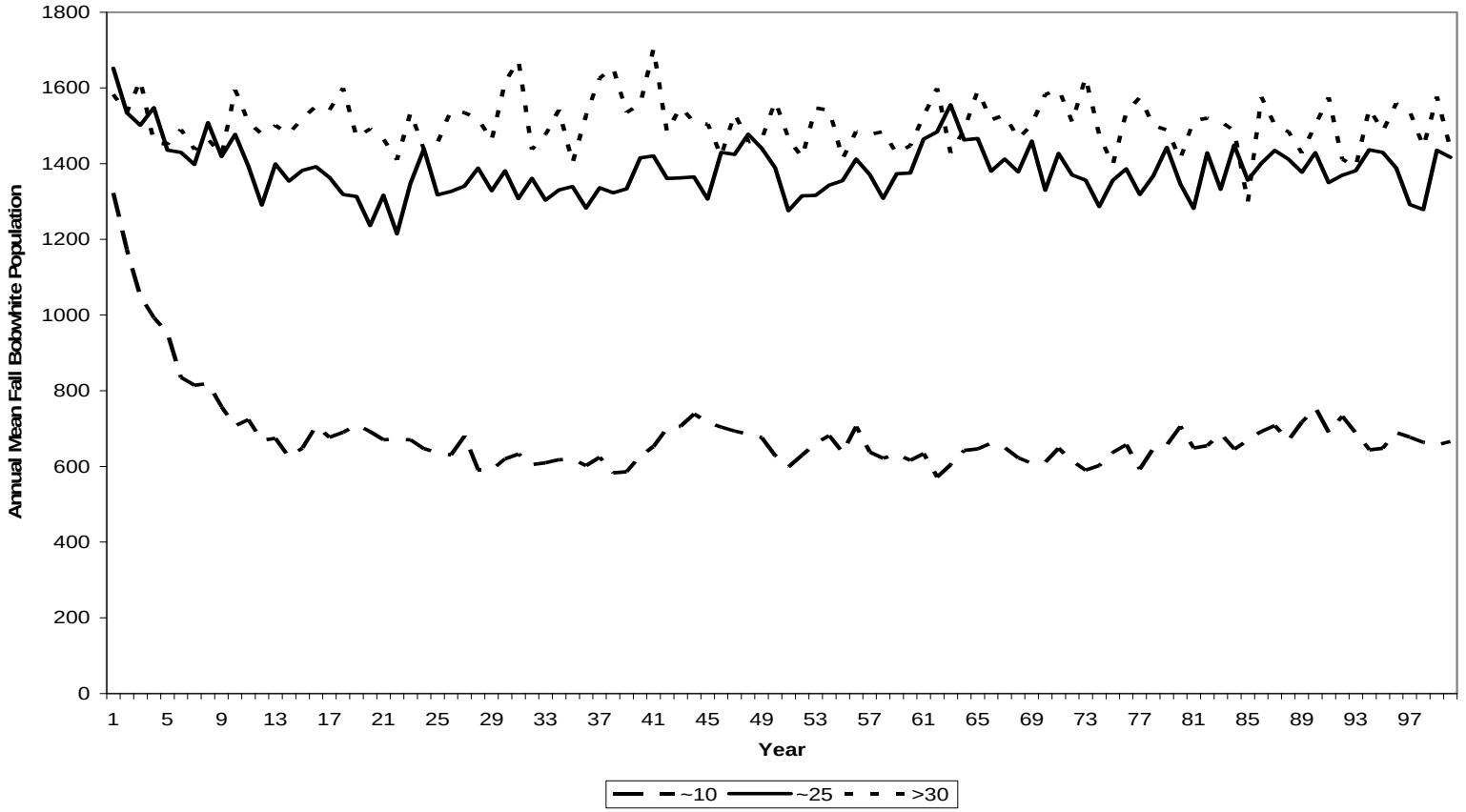

Figure 4.1. Simulated long-term trend for fall bobwhite populations in areas with 10%, 25%, and >30% brush canopy coverage, Brooks County, Texas, USA.

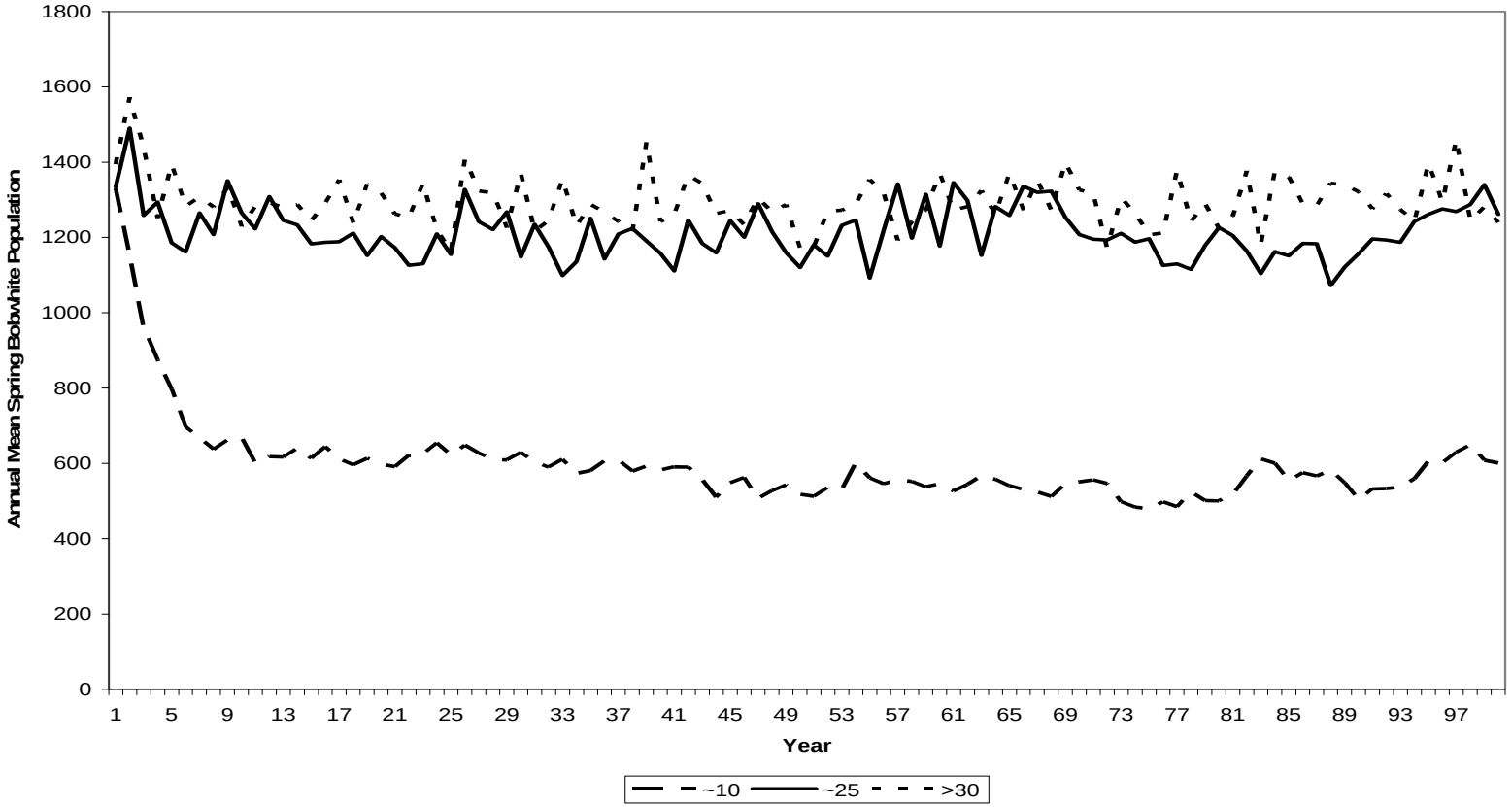

Figure 4.2. Simulated long-term trend for spring bobwhite populations in areas with 10%, 25%, and >30% brush canopy coverage, Brooks County, Texas, USA.

classes than in the ~10% BCC class (54.2%) using a quasi-extinction criterion of ≤40 birds (≤0.05 birds/ha).

DISCUSSION

Numerous studies have reported on habitat use for bobwhites (Kopp et al. 1998, Guthery et al. 2000*b*, Hiller and Guthery 2005, Arredondo et al. 2007). My study is the first to relate habitat with demographic performance. It is intuitive that density, productivity, and survival would be optimum at some point within the bounds of selection. Such a finding would indicate a component of quality to habitat. However, Guthery (1997) argued against the existence of habitat quality and stated that quantity of usable space was the principal determinant of population persistence and density. That is, that habitat was either usable or not usable and, if the habitat was usable, then density would fluctuate because of stochasitic events, but not habitat quality. Increasing the quality of useable habitat would not result in an increase in density. Guthery's (1997) hypothesis therefore would predict that demographic parameters would not vary within the bounds of selection.

My data provide an indirect test of Guthery's (1997) usable space hypothesis. I know that the habitat on my study area is usable for bobwhites. Bobwhite populations have persisted at moderate to high densities on this large, contiguous landscape for at least the past 70 years (Lehmann 1984). Thus, Guthery's (1997) hypothesis would be supported if demographic parameters did not vary among BCC classes. I documented that demographic parameters did differ among cover classes.

Simulated fall and spring population sizes increased with increasing brush canopy cover. In addition, fall and spring population persistence followed this same trend. Chick production was the primary parameter driving population size and persistence. Chick production at the ~25% and >30% BCC classes were nearly double the chick production at the ~10% BCC class. Therefore, my findings appear to lend support that there may still be a component of habitat quality even within the context of usable space as defined by Guthery (1997).

A possible reason why I did not observe any differences among the 3 BCC classes in my univariate analysis was that the composition and structure of other habitat components on the 3 treatments could have differed. Guthery (1999) defined 3 sources of "slack" as it relates to bobwhite habitat management where landscapes with different patch configurations could lead to fully usable space. One source of slack is the interchangeability of functions provided by woody and herbaceous cover. This interchangeability permits canopy coverage of woody and herbaceous plants to vary among landscapes, with space-time saturation remaining constant (i.e., landscapes may be of similar quality, but have variable quantities of patch types). The possible occurrence of slack could have minimized the likelihood of detecting demographic differences among the 3 BCC classes.

An interesting finding of my study is that none of the demographic parameters differed among the 3 BCC classes when compared univariately, but a long-term, cumulative effect was detected. The >30% BCC treatment had the highest fall and spring populations followed by the ~25% and ~10% BCC class. Moreover, probability

of population persistence also decreased with decreasing cover. The importance of this finding is that most wildlife management decisions are based on short-term effects of habitat. If short-term and long-term effects of habitat have differing effects on demographic performance, potential negative effects of erroneous management decisions may not be noticed or addressed until years later.

In conclusion, based on a univariate analysis bobwhite density, production, and survival were similar among the 3 BCC treatments, however results from simulation modeling indicated that ~25% and >30% BCC classes had long-term effects on population parameters. Further research is needed to investigate the impact of higher levels of BCC on the demographic parameters I estimated. My study indicates that if managers choose, they can manage properties similar to my study area with about 30% BCC without fear of harming the bobwhite populations on their properties. One caveat is that I only had BCC treatments at the lower end of the BCC range utilized by bobwhites. Bobwhites will utilize BCC of ~5% (Guthery 1986:18) to ~80% (Schroeder 1985, Kopp et al. 1998). My study could have been improved if the BCC treatments would have included cover classes in the higher end of the range. A broader range of cover classes would have allowed for wider inferences, but such a study was not logistically feasible in my study area.

MANAGEMENT IMPLICATIONS

On areas similar to my study area, managers wanting to maximize fall bobwhite populations should manage for ~30% BCC. However, managers may have other management priorities other than just maximizing the fall bobwhite populations.

Additional priorities may include increasing forage production for cattle grazing and/or decreasing BCC for easier accessibility for hunting purposes, and/or more open areas for easier, better shooting, and/or aesthetic values related to hunting, such as being able to see hunting dogs search for prey. Regardless of the amount of BCC that is managed for, managers need to consider the distribution of woody cover to make sure it meets what is required by bobwhites and to not focus on one component of bobwhite habitat, because different habitat components can sometimes be used interchangeably by bobwhites (Guthery 1999).

CHAPTER V

SUMMARY AND CONCLUSIONS

Northern bobwhite nest-site location is a nonrandom process. Bobwhite nests tend to be situated in taller and denser vegetation than would be expected if nest-site location was a random process. The nest-concealment hypothesis, the concept that better nest concealment reduces predation risk, traditionally has been the common explanation for this nonrandom process. I tested this hypothesis using a 5-year dataset of northern bobwhite nests (n = 253) in southern Texas during 2001–2005. I compared 4 microhabitat variables (nest-clump diameter, nest-vegetation height, volume of cover, and suitable nest-clump density) between successful (n = 135) and depredated nests (n = 118). I documented similar microhabitat attributes between successful and depredated nests. Discriminant function analysis indicated nest–vegetation height was the most important variable discriminating between nest fates followed by volume of cover. However, the discriminant function correctly classified only 48 to 59% of nest fates into the correct group (Eigenvalue = 0.035, Wilk's lambda = 0.97, P = 0.0139), a classification result no better than chance alone (Kappa statistics, P > 0.8628). In addition, the discriminant function explained only 18% of the variation in nest fate. Thus, my results did not support the nest-concealment hypothesis. In light of these findings, I recommend managing for increasing the amount of adequate nesting cover and not habitat with specific nest-fate attributes.

Models are important tools that can help managers and researchers understand population dynamics of a species and how different habitat and/or population management scenarios impact that species. I used radio-telemetry data from 2000–2005, part of a long-term, northern bobwhite study in southern Texas, to develop a stochastic simulation model for bobwhite population on the 800-ha study area in the Rio Grande Plains. The model is based on difference equations (Δt = 3 months), with stochastic variables drawn from Weibull distributions. I ran simulations for 100 years using STELLA® 9.0.2 and evaluated the model by comparing simulation results with empirical estimates of 6 population parameters (female- and male-adult annual survival, fall and spring density, finite rate of increase [λ], and winter age ratios). Using a quasi-extinction criteria of ≤40 birds (≤0.05 birds/ha), the probability of persistence for 100 years for the spring population was 74.2% and 72.5% for the fall population. Using a less restrictive quasi-extinction criteria (≤14 birds) used by other researchers, the probability of persistence for the spring population was 91.7% and 91.7% for the fall population. Simulated population parameters were similar to those observed in the field for 5 of 6 population parameters. Only simulated male adult annual survival ($\bar{x}$ = 0.04, SE = 0.007) differed by 275.0% from field estimates ($\bar{x}$ = 0.15, SE = 0.036). Despite this difference, my model appears to be a good predictor of bobwhite populations in the Rio Grande Plains of Texas.

Much research has been devoted to quantifying the habitat needs and selection for many wildlife species. However, how habitat selection affects the long-term demographic performance of a species has been ignored. I used northern bobwhite and

brush canopy coverage an important habitat component to evaluate the influence of habitat on short- and long-term demographic performance of the species. I obtained estimates of bobwhite density, survival, and production (proportion of hens nesting, nesting attempts per hen, and clutch size) in 3 study areas with ~10%, ~25%, and >30% brush canopy coverage (BBC). I estimated bobwhite density during October and March using helicopter surveys and estimated survival and production using radio-telemetry data from a long-term (2001–2005), northern bobwhite study in southern Texas. All demographic parameters were similar among the 3 BCC classes. However, simulation modeling indicated that long-term demographic performance was greater on the ~25% and >30% BCC classes. These 2 cover classes had higher fall and spring bobwhite populations than the ~10% BCC classes. In addition, the probability of fall population persistence was greater in the ~25% (90.8%) and >30% (100.0%) BCC classes than the ~10% cover class (54.2%) using a quasi-extinction criterion of ≤40 birds (≤0.05 birds/ha). My study highlights the shortcoming of considering only short-term effects when comparing habitat given that short- and long-term effects of habitat on demographic performance can differ.

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APPENDIX A

PARAMETER AND VARIABLE DEFINITIONS USED IN THE MODEL TO SIMULATE NORTHERN BOBWHITE POPULATIONS IN SOUTHERN TEXAS

Parameter or variable	Definition
A	= geographic area of interest simulated by the model.
BHatchSeason	= bounds the proportion of nests that hatch during the spring season (1 Mar–31 May) and summer season (1 Jun–31 Aug) between 0.0 and 1.0.
BM_{FASp}	= bounds M_{FASp} between 0.00 and 0.80.
BM_{FASu}	= bounds M_{FASu} between 0.00 and 0.78.
BM_{FAFa}	= bounds M_{FAFa} between 0.00 and 0.57.
BM_{FAWi}	= bounds M_{FAWi} between 0.00 and 0.75.
BM_{FJSp}	= bounds M_{FJSp} at 0.48.
BM_{FJSu}	= bounds M_{FJSu} at 0.48.
BM_{FJFa}	= bounds M_{FJFa} between 0.00 and 0.45.
BM_{FJWi}	= bounds M_{FJWi} between 0.00 and 1.00.
BM_{MASp}	= bounds M_{MASp} between 0.00 and 0.70.
BM_{MASu}	= bounds M_{MASu} between 0.18 and 0.82.
BM_{MAFa}	= bounds M_{MAFa} between 0.00 and 0.43.
BM_{MAWi}	= bounds M_{MAWi} between 0.00 and 1.00.

Parameter or variable	Definition
BM_{MJSp}	= bounds M_{MJSp} at 0.48.
BM_{MJSu}	= bounds M_{MJSu} at 0.48.
BM_{MJFa}	= bounds M_{MJFa} between 0.00 and 0.20.
BM_{MJWi}	= bounds M_{MJWi} between 0.00 and 1.00.
Breed	= number of adult females entering the spring breeding season (1 Mar–31 May).
BreedPop	= total number of adult, male and female bobwhites in the spring (1 Mar–31 May) and summer (1 Jun–31 Aug) breeding populations.
Chicks	= number of chicks produced during spring (1 Mar–31 May) and summer (1 Jun–31 Aug).
Clutch	= clutch size.
Δt	= time step from t to $t + 1$ (3 months or 1 season).
DD_R	= density–dependent reproduction, a density–dependent feedback loop that scales the relationship between the breeding population (female and male, adults) and production during the spring (1 Mar–31 May) and summer (1 Jun–31 Aug) seasons.
DD_{Wi}	= density–dependent winter mortality, a density–dependent feedback loop that scales the relationship between the winter

Parameter or variable	Definition
	population (female and male, adult and juvenile) and mortality during the winter (1 Dec–28 Feb) season.
F_A	= number of female, adults in each Δt.
F_J	= number of female, juveniles in each Δt.
F_{JProd}	= number of female, juveniles produced during spring (1 Mar–31 May) and summer (1 Jun–31 Aug).
Hatch	= calculates the proportion of nests hatched during the spring season (1 Mar–31 May; *BHatchSeason*) and the summer season (1 Jun–31 Aug; 1 - *BHatchSeason*).
HatchSeason	= the proportion of nests that hatch during the spring season (1 Mar–31 May).
M_{FA}	= number of female, adults dying in each Δt.
M_{FASp}	= female, adult mortality during the spring (1 Mar–31 May) season.
M_{FASu}	= female, adult mortality during the summer (1 Jun–31 Aug) season.
M_{FAFa}	= female, adult mortality during the fall (1 Sep–30 Nov) season.
M_{FAWi}	= female, adult mortality during the winter (1 Dec–28 Feb) season.
M_{FJ}	= number of female, juveniles dying in each Δt.

Parameter or variable	Definition
M_{FJSp}	= female, juvenile mortality during the spring (1 Mar–31 May) season.
M_{FJSu}	= female, juvenile mortality during the summer (1 Jun–31 Aug) season.
M_{FJFa}	= female, juvenile mortality during the fall (1 Sep–30 Nov) season.
M_{FJWi}	= female, juvenile mortality during the winter (1 Dec–28 Feb) season.
M_{MA}	= number of male, adults dying in each Δt.
M_{MASp}	= male, adult mortality during the spring (1 Mar–31 May) season.
M_{MASu}	= male, adult mortality during the summer (1 Jun–31 Aug) season.
M_{MAFa}	= male, adult mortality during the fall (1 Sep–30 Nov) season.
M_{MAWi}	= male, adult mortality during the winter (1 Dec–28 Feb) season.
M_A	= number of male, adults in each Δt.
M_J	= number of male, juveniles in each Δt.
M_{JProd}	= number of male, juveniles produced during spring (1 Mar–31 May) and summer (1 Jun–31 Aug).
M_{MJ}	= number of male, juveniles dying in each Δt.
M_{MJSp}	= male, juvenile mortality during the season.

Parameter or variable	Definition
M_{MJSu}	= male, juvenile mortality during the summer (1 Jun–31 Aug) season.
M_{MJFa}	= male, juvenile mortality during the fall (1 Sep–30 Nov) season.
M_{MJWi}	= male, juvenile mortality during the winter (1 Dec–28 Feb) season.
$MRate_{FA}$(t)	=female adult mortality rate, which depends on the season (if *Season* = 1 then M_{FAWi}; if *Season* = 2 then M_{FASp}; if *Season* = 3 then M_{FASu}; if *Season* = 4 then M_{FAFa})
$MRate_{FJ}$(t)	=female juvenile mortality rate, which depends on the season (if *Season* = 1 then M_{FJWi}; if *Season* = 2 then M_{FJSp}; if *Season* = 3 then M_{FJSu}; if *Season* = 4 then M_{FJFa}).
$MRate_{MA}$(t)	=male adult mortality rate, which depends on the season (if *Season* = 1 then M_{MAWi}; if *Season* = 2 then M_{MASp}; if *Season* = 3 then M_{MASu}; if *Season* = 4 then M_{MAFa}).
$MRate_{MJ}$(t)	=male juvenile mortality rate, which depends on the season(if *Season* = 1 then M_{MJWi}; if *Season* = 2 then M_{MJSp}; if *Season* = 3 then M_{MJSu}; if *Season* = 4 then M_{FJFa}).
NestAttempt	= number of nesting attempts per adult female that enter the nesting season and nest during that nesting season (spring, 1 Mar–

Parameter or variable	Definition
	31 May and summer, 1 Jun–31 Aug), regardless of whether they survive the nesting season.
NestSurv	= estimate of daily nest survival (0.9593) from Radar et al. (2007), raised to the 23 power to estimate nest survival for the 23-day incubation period.
Prod	= transfers the chicks produced during the spring (1 Mar–31 May) and/or the summer (1 Jun–31 Aug) nesting seasons into the stock variable *C* at the beginning of the spring and summer seasons.
PropNest	= the proportion of adult female bobwhites that enter the nesting season and nest during the spring (1 Mar–31 May) and/or the summer (1 Jun–31 Aug) nesting seasons, regardless of whether they survive the nesting season.
Repro	= calculates the number of chicks produced during the spring (1 Mar–31 May) and/or the summer (1 Jun–31 Aug) nesting seasons.
Season	= counter that represents the 4 seasons in a year with 1 = winter (1 Dec– 28 Feb); 2 = spring (1 Mar–31 May); 3 = summer (1 Jun–31 Aug); and 4 = fall (1 Sep–30 Nov).
S_{FJ}	= number of female, juveniles surviving in each Δt, move to the adult cohort during winter (1 Dec–28 Feb).

Parameter or variable	Definition
S_{MJ}	= number of male, juveniles surviving in each Δt, move to the adult cohort during winter (1 Dec–28 Feb).
WiPop	= number of female adult, female juveniles, male adults, and male juveniles during winter (1 Dec–28 Feb).

APPENDIX B

PARAMETERS USED IN THE WEIBULL DISTRIBUTIONS FOR THE STOCHASTIC NORTHERN BOBWHITE POPULATION MODEL

Parameter	β	α	γ
Clutch	14.306	4.988	0.000
PropNest	25.289	1.569	42.827
NestAttempt	0.766	1.361	0.975
M_{FJFa}	1.013	8.532	0.000
M_{FJWi}	0.417	1.000	0.000
M_{MJFa}	1.013	8.532	0.000
M_{MJWi}	0.417	1.000	0.000
M_{FASp}	0.461	2.109	0.136
M_{FASu}	0.547	2.864	0.125
M_{FAWi}	0.642	2.278	0.106
M_{MASp}	0.440	2.418	0.226
M_{MAFa}	0.417	1.000	0.000
M_{MAWi}	1.144	4.719	0.000

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